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EFFECTS OF THE FEDERAL COLUMBIA RIVER POWER SYSTEM ON SALMON POPULATIONS

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INTRODUCTION

The construction and operation of the 31 Federal Columbia River Power System (FCRPS) dams have contributed to the decline of anadromous salmon populations in the Columbia River basin and continues to affect them (see Fig. 1 for major dams in the Columbia River basin - not all FCRPS dams). While the dams provide about 60 percent of the Pacific Northwest region's hydroelectric generating capacity, supply irrigation water to more than a million acres of land, and store water to enhance flood control, they also block access to historic spawning areas or alter the migratory corridor leading to increased direct and indirect mortality. In addition to the FCRPS, human impacts from construction of hundreds of other dams, harvest, mining and dredging, and agricultural practices, have affected various stocks of Columbia River basin anadromous salmon populations. Thus, ascribing effects of the FCRPS is complicated. Although many physical and operational changes have occurred since the completion of the FCRPS dams in an attempt to minimize impacts on anadromous salmon populations, and research has shown that increases in direct survival of salmonids migrants has occurred from these changes, deleterious effects from having passed through the FCRPS express themselves indirectly downstream of the hydropower system to an unknown degree. Determining the extent to which direct an indirect effects of the hydropower system negatively affect salmon populations, in the context of all other factors influencing salmon populations, is critical for defining additional measures needed within the FCRPS to assure salmon survival. Although we can measure direct survival and travel time of fish on an annual basis, inferences on delayed mortality often rely on long-term trends in return rates of adult fish, and these data are inherently variable. Thus, estimating the extent to which the FCRPS and the sum of all other human-induced activities affects salmon populations requires trying to tease out an understanding of direct and indirect affects in concert with the natural variability in salmon population trends. Our knowledge of natural salmon variability through time is lacking, but the historical record provides some indications of its magnitude.

Historical Background

The size of all animal populations fluctuate. For salmon, we most often associate our activities to their population trends, and in many cases, rightly so. However, we generally lack knowledge of natural population fluctuations independent of human interactions. Despite a long Native American oral history in the Pacific Northwest, little information exists on the size and extent of salmon population fluctuations. Estimates of annual adult salmon returns to the Columbia River basin in the last couple of centuries have ranged from 7.4 to 8.8 million fish (Chapman 1986). Of these, Chapman (1986) estimated that spring and summer chinook salmon numbered 500-590 thousand, and 2-2.5 million, respectively. However, at the end of the last ice age (approximately 15,000 years before the present), glaciers covered most of the upper Columbia River and much of the Salmon River drainage (McPhail 1986). Thus, these salmon populations are fairly recent in origin. Chatters et al. (1995)concluded that over the past 7,000 years, salmon production in the Columbia basin has varied tremendously with changes in climate. They speculated that average salmon populations were much lower approximately 3,500 years ago compared to recent centuries, but higher 1,200 years before the present. These speculations comport with recent findings of Finney et al. (2002) for Alaska sockeye salmon populations.

Anecdotal evidence indicates that natural variations in Columbia River salmon abundance also occurred over shorter time spans. Chance (1973) quotes from a number of early diaries that in 1811 and again in the late 1820s salmon populations from the middle Columbia River (between the confluence of the Snake River and Kettle Falls) were so low that settlers and native Americans relied on horse flesh for survival. Although Snake River basin salmon populations were also probably also low at this time, based on catch records for the Columbia River basin as a whole, all stocks rebounded to high levels near the end of the century. At that time, dramatic declines in Columbia River salmon populations began as a result of overfishing, exacerbated further beginning early in the 20th century by environmental degradation from mining, grazing, logging, water withdrawals for irrigation, and dams constructed on major tributaries for power production and water storage. Although stocks decreased, a signal of variability in run size still existed. The upriver run (above Bonneville Dam) of spring chinook salmon averaged 119,000 fish from 1940-1949 (with an average harvest rate of 60%), increased to 208,000 fish from 1950-1959 (with an average harvest rate of 60%), and decreased to 171,000 from 1960-1969 (with an average harvest rate of 39%) Status Report, Columbia River fish runs and fisheries - available at:
http://www.dfw.state.or.us/ODFWhtml/InfoCntrFish/InterFish/crm.html#annual

Impacts From Dams

Concerns about the potential impacts of the FCRPS on anadromous fish were raised prior to the construction of Bonneville Dam (Griffin 1935). In fact, with the dam's completion, studies began in 1939 to estimate survival through turbines and spill for juvenile salmon passing the project to determine the dam's affect on juvenile salmon (Harlan B. Holmes, unpublished U.S. Bureau of Commercial Fisheries Report). Results from these studies and those by Schoeneman and Junge (1961)at McNary Dam in the mid-1950s led to concern about the probable impact that dams had on juveniles. As five additional dams were scheduled for construction on the mainstem Columbia and Snake Rivers, a Fish Passage Program within the Bureau of Commercial Fisheries (now NOAA Fisheries), began studies to determine the adaptability of salmon to new environments created by dams, effects of impoundments on fish migration, affects to migrants from dam passage, and means to mitigate for effects.

Raymond (1979) provided the initial summary of changes in survival and travel time for yearling migrants that occurred during and after dam completion. In short, the 1966 to1968 average annual survival of wild yearling chinook salmon outmigrants from a trap on the Salmon River to Ice Harbor Dam averaged approximately 89% (Lower Monumental, Little Goose, and

Lower Granite Dams were not yet completed) and the 1966 and 1967 (prior to completion of John Day) survival from Ice Harbor to The Dalles Dam averaged 64%. Combining these two estimates with an estimated survival between The Dalles and Bonneville Dam provided overall juvenile chinook salmon and steelhead survival estimates ranging between approximately 40-55% through what now constitutes the mainstem FCRPS dams (with 4 dams in place) (Williams et al. 2001). After completion of the system (with 8 dams in place), survival estimates for yearling chinook salmon and steelhead decreased to mean values of approximately 16 and 11%, respectively (but near 0 for both in the very low-flow year of 1977) (Williams et al. 2001).

Reservoirs behind dams increased travel time for juvenile migrants. Annual travel time estimates for fish were 10d (high flow) to 20d (low flow) to migrate though the hydropower system with 4 mainstem dams in place (expansion of data from (Raymond 1979), but after completion of all 8 dams, annual travel time estimates ranged from 15d (high flow) to 40 d (low flow). Concurrent with research documenting direct affects of the dams on fish, other researchers worked on means to mitigate for them. This research led the U.S. Army Corps of Engineers (COE) to construct juvenile bypass systems at dams, modify spillways, and implement a transportation program to collect fish at upstream dams and barge them to a release site below Bonneville Dam.

Despite these efforts, by the early to mid-1990s, stocks had not recovered. As a consequence, 12 of 16 Columbia River basin Evolutionarily Significant Units (ESUs) (Waples 1991) were listed as threatened or endangered under the Endangered Species Act (ESA) (April 22, 1992: 57 FR 14653).

The PATH Process

To provide information needed to write Biological Opinions associated with the stock listings, and develop estimates of FCRPS impacts, in 1995, NOAA Fisheries (NMFS) created the Plan for Analyzing and Testing Hypotheses (PATH). A summary of the PATH process based on a paper by Marmorek and Peters (2001) follows.

A group of approximately 30 scientists worked for nearly 5 years to develop analyses to explain the impact of the FCRPS on anadromous fish stocks above Bonneville Dam. PATH scientists identified two key uncertainties that most strongly affect survival and recovery potentials of Snake River spring/summer and fall chinook salmon: extra mortality of in-river migrants, and the relative post-Bonneville survival of transported fish compared to post-Bonneville survival of in-river migrants (designated as “D”).

Extra mortality was a construct of the models used by PATH, a parameter used to account for any mortality occurring outside the juvenile migration corridor not accounted for by the other terms used in the PATH life cycle models (such as, productivity and carrying capacity, mortality in reservoirs and at dams, and estuarine/ocean mortality affecting all salmonid populations). The existence of extra mortality required the presumption that changes in ocean conditions had the same relative impact on productivity for all upstream and downstream Columbia River stocks. No direct measurements of extra mortality existed, and it was only inferred from other measured quantities. As the observed historical patterns in extra mortality were linked with several possible causes, PATH formulated three alternative hypotheses concerning extra mortality and the possibility of actions within the FCRPS to decrease it:

a. "Hydro" – extra mortality resulted from adverse effects to smolts from migrating through the 8 mainstem dams of the FCRPS. Removal of dams in the Snake River would eliminate extra mortality.
b. "Regime shift" – extra mortality follows a 60-yr cycle related to long-term cycles in ocean conditions. No FCRPS actions will directly reduce extra mortality, but extra mortality will eventually dissipate when ocean conditions improve.
c. "Stock viability" – extra mortality resulted from processes not affected by any FCRPS action or regime shift. Stocks will remain low due to interactions with hatchery fish, the presence of diseases such as Bacterial Kidney Disease, or reduction in nutrients associated with historical declines in spawning stock.

In the PATH models, "D" represented an annual value of the differential survival downstream of Bonneville Dam for transported fish compared to in-river migrants. Low values of "D" indicated that transportation did not provide full mitigation for losses at dams; that is, transported fish incurred greater mortality downstream of Bonneville Dam than did in-river migrants. Further, if a low enough value of "D" existed it explained historical patterns of stock productivity without the need to require extra mortality to explain changes in productivity.

Many PATH participants felt that extra mortality existed; however, consensus among the group that it did, or causes as to why, was never reached. Arguments for the existence of extra mortality and its linkage to the FCRPS were made by Schaller et al. (1999; 2000), Deriso et al. (2001), Petrosky et al. (2001), and Budy et al. (2002). Zabel and Williams (2000) suggested that differences in productivity could have occurred as a result of differences in underlying stock responses to changing ocean conditions. Subsequent to PATH, Levin and Tolimieri (2001) and Levin(2003)found that chinook salmon populations used in the PATH life cycle models, Snake, Upper Columbia, and middle Columbia, had different productivity, and productivity varied between different time periods, but not consistently with changes in ocean conditions. The degree to which the hydropower system affects survival of fish that successfully survived to below Bonneville Dam remains contentious. We provide a more detailed discussion of this mortality in the section on Latent Mortality (see below).

Evaluations of Stocks Subsequent to PATH

Due to perceived complexity of PATH products by some Northwest Fisheries Science Center scientists not involved with PATH, a matrix model was developed in mid- to late 1999 to evaluate the status of listed Snake River spring-summer chinook salmon stocks. The results of the matrix modeling process indicated that little room to increase stock productivity existed within the migration corridor of the FCRPS because of improvements made at dams between the mid-1970s and late 1980s. Results indicated that factors currently driving productivity occurred in the freshwater spawning and rearing areas and in estuary/early ocean residence (Kareiva et al. 2000). The matrix model set a value for "D" at 0.7, and used a range of values for delayed mortality.

Concurrent with matrix-modeling efforts, other NWFSC staff developed draft "White Papers" to summarize knowledge about FCRPS affects to stocks. After considering comments based on regional review, final versions of the "White Papers" were posted on the NWFSC website: http://www.nwfsc.noaa.gov/publications/whitepapers/index.cfm. The "White Papers" covered the following:

1) "Passage of Juvenile and Adult Salmonids Past Columbia and Snake River Dams,"
2) "Predation on Salmonids Relative to the Federal Columbia River Power System,"
3) "Salmonid Travel Time and Survival Related to Flow in the Columbia River basin," and
4) "Summary of Research Related to Transportation of Juvenile Anadromous Salmonids Around Snake and Columbia River Dams".

In developing the NMFS 2000 FCRPS BiOp, the Biological Effects Team reviewed and analyzed fish passage assumptions used by NMFS in earlier fish passage modeling exercises, those developed in the PATH process, fish passage information contained in the four "White Papers", and the most recent empirical data to determine the fish passage parameters for input into the Simulated Passage (SIMPAS) model. To develop a new BiOp, NOAA Fisheries needs an update on affects of the FCRPS on ESA listed salmonids in the Columbia River basin. In this Tech Memo we provide an update on hydropower system survival for listed juvenile and adult salmon through the mainstem Snake and Columbia River dams (to the extent data are available), results from transportation studies, flow effects on survival and travel time, and overall effects of FCRPS operations on adult returns. We focus primarily on Snake River spring-summer chinook salmon, as these fish migrate through the entire FCRPS mainstem dam complex and we have the most data about these stocks. Fewer data exist for all other stocks, so we either provide incomplete information or make inferences where we deem reasonable.

Returns of many listed Columbia River salmon stocks in the last several years have far exceeded numbers seen in recent decades. Thus, we also discuss associations between direct survival through the FCRPS and changes in adult returns. Again, we do this most effectively for Snake River spring-summer chinook salmon, as we have the best measure of their population fluctuation over time. For other stocks, we mostly relied on changes in combined wild and hatchery adult returns to dams, as reliable estimates of wild adult returns and smolts do not exist.

The following sections provide summaries of methods and results from work contained in recent annual reports to the COE and BPA, or in peer-reviewed literature. We direct readers who want additional information to those sources. In a few cases, some of this work is not readily available as it is contained in manuscripts under review or "in press". We will provide additional details of this information, on request.

General Basis For Analyses

We believe annual smolt-to-adult return rates (SARs) of fish populations provide the most valuable information about potential influences of the FCRPS on salmon populations. Thus, we first present SARs for unmarked populations, where available. Unmarked populations of fish, however, cannot inform us about any of the particular processes affecting fish as juveniles. To develop this information, we relied mainly on analyses of PIT-tagged fish. Tagging juvenile salmonids with PIT tags began on a small scale in 1987 and has expanded tremendously since that time, although not homogeneously throughout the Columbia River basin (Table 1.) Further, the fish tagged did not always represent the run or rearing type for the general population of a species. Between 1989 and 2001, the majority of PIT-tagged fish were Snake River spring/summer chinook salmon. Some studies PIT tagged fish as they passed discrete points along the migration corridor, while others tagged fish only in certain natal streams or hatcheries, or tagged the same number in each stream or hatchery regardless of the total number of fish available. This left other streams or hatcheries unmarked or under represented in the sample population. Twenty different organizations have PIT tagged fish in the basin. By far, NOAA Fisheries has PIT tagged the majority of fish (ca. 5.2 M) , followed by U.S. Fish and Wildlife Service (USFWS) (ca.1.1 M), and Idaho Fish and Game (IDFG) (ca. 1.0 M), to as few as ca. 235 by Columbia Intertribal Fisheries Commission (CRITFC).

Table 1. Annual numbers of fish PIT tagged and released in different areas of the Columbia River basin.

Outmigration year	Upper Columbia River[a]	Snake River	Middle Columbia River[b]	Lower Columbia River[c]	Willamette River
1987	7673	2619	-	-	-
1988	-	19728	25088	-	-
1989	4998	92254	22894	-	-
1990	7857	66804	22099	1700	-
1991	6644	70462	32613	724	-
1992	11021	66144	30645	1002	-
1993	24326	132409	29693	733	-
1994	33916	335845	1853	721	1775
1995	34982	514551	-	-	-
1996	46213	373356	3044	2980	-
1997	40153	458881	107685	10708	-
1998	147133	589815	200595	12666	-
1999	168593	763014	477897	18336	3429
2001	214688	561453	178734	33025	7791
2002	613296	858240	223181	59511	9597
2003	1023730	907460	121805	124748	3927
Total	2385223	5813035	1477826	266854	26519

[a] drainage above the confluence with the Yakima River (above RKm 539)
[b] drainage between the confluence with the Wind and Yakima Rivers (between RKm 252-539)
[c] drainage from the Wind River to the ocean (below RKm 252)

ADULT RETURN RATES

Based On Non-tagged Fish

Methods

Smolt-to-adult return rates (SARs) provide a measure of survival that encompasses smolt migration, estuary/ocean residence, and adult return stages. Where possible we calculated this by dividing returning adults from a single brood year by smolts from the brood year. The changes in

SARs over an extended number of years provided an index of temporal variability in stock productivity. For Snake River spring-summer chinook salmon, we estimated recent SARs from Lower Granite Dam, and compared them with earlier years by adjusting for annual downstream harvest. We then used these estimates to compare to estimates of SARs (catch plus escapement) to the upper Snake River dam in earlier years. In brief, from Petrosky et al. (2001) we used estimated wild adult (1-, 2-, and 3-ocean fish) returns from 1964 to 1996 (we adjusted 1993 to 1996 1-ocean fish for estimated additional returns to Oregon) and harvest rates from 1964 to 1999. We used Raymond (1988) for estimates of smolt abundance between 1964 and 1984. We derived estimates for wild smolts from 1993 to 2003 by expanding the daily collection of wild fish at Lower Granite Dam (http://www.fpc.org/smoltqueries/HistoricDailyData.asp) by the daily estimates of detection efficiency (derived with (Sandford and Smith 2002)methodology) of wild smolts at the dam for each year. For smolt years 1995 to 2003, we adjusted smolt estimates by an estimated percentage of non-clipped hatchery fish arriving at the dam not identified as hatchery origin. This adjustment decreased numbers of wild smolts by 6, 1, 0, 2, 4, 3, 1, 4, and 4% for smolt years 1995 through 2003, respectively. We estimated smolt abundance from 1985 to 1993 based on a Beverton-Holt curve generated from estimated numbers of smolts from 1964 to1984 and 1994 to 2003 ($R^2 \cong 0.80$) and the number of wild fish passing the upper Snake River dam 2 years earlier. We derived the estimated wild adult returns to Lower Granite Dam from 1997 through 2003 from annual fish counts of spring-summer chinook salmon reported to have passed the dam. Fish counters at the dam enumerated fish as they passed through the counting window and assigned them to either a group with adipose fins (ostensibly wild fish) or a group without adipose fins (known hatchery fish with fins clipped as juveniles). We adjusted the clipped (missing adipose fin) hatchery fish returns by the estimated proportion of non-clipped (fish with an adipose fin, but possibly with other clipped fins) hatchery fish in the return. We used estimates of 89.6, 87.7, 86.5, 96.0, 92.3, 89.6, and 88.9 % for identifiable adult (2- and 3-ocean fish) hatchery fish in return years from 1997 through 2003, respectively. We then subtracted the corrected hatchery count from the total adult return to derive the wild fish estimate.

To separate adult returns into the respective 2- and 3-ocean component, we used two methods. For the 1997 return year, we used PIT-tag data to estimate the percentage of 3-ocean fish that returned from the 1994 outmigration. We expanded the estimated number of jacks plus 2-ocean fish from the 1994 outmigration (data from (Petrosky et al. 2001)to derive the number of 3-ocean fish to meet the estimated percentage in the return. We then subtracted this estimate from the estimate of wild 1997 adults to derive the number of 2-ocean fish. For returns from 1998 through 2003, we used age-class data collected by Idaho Department of Fish and Game (IDFG) [1998-2001 data from Kiefer et al.(2002); 2002-2003 date, unpublished IDFG]. We then estimated the total adult return for outmigration years from 1995 through 2001 (only through 2-ocean returns for the last year) by combining the estimated number of wild jacks with the 2- and 3-ocean returns for each year. To account for harvest rates in the Columbia River that varied between 0 and 40% over the time period, we expanded adult returns to the uppermost Snake River dam for the period between 1964 and 1999 based on estimated Columbia River harvest rates in Petrosky et al. (2001). We expanded adult returns for 2000 to 2003 based on unpublished harvest rates (Peter Dygert, NOAA Fisheries, personal communication).

For Snake River yearling chinook salmon, in addition to SARs based on Petrosky et al. (2001), we plotted SARs for the period from 1964-1984 from Raymond (1988).

For Snake River steelhead, we used Raymond's (1988) SAR estimates for the period from 1964 to 1984. We used Charlie Petrosky's (IDFG) updated steelhead SARs from 1985 to1994 submitted as part of the PATH process (Marmorek et al. 1998b). Charlie Petrosky (IDFG, personal communication) used the same methods used in the PATH report to develop preliminary SAR estimates for the period 1995 to 2000 for Subbasin Planning. He cautioned these estimates are preliminary updated wild adult and smolt numbers, not yet reviewed by the Snake River Technical Recovery Team. For his recent analyses, NOAA Fisheries provided the 1997-2000 estimated wild smolt numbers to the Technical Advisory Committee (TAC) (via Peter Dygert, NOAA Fisheries, Northwest Regional Office). Adult wild A-run and B-run estimates were also from TAC. Updated adult-age structure information was from LGR scale sampling for 1995-2001 run years (Cooperators: NMFS and IDFG--data collection & archiving; USFWS and Utah State University--scale reading).

For stocks where we lacked direct juvenile and adult information for wild stocks, we compared the median count of adult fish from the 2001 to 2003 return years to the median adult count from the 1992 to 2000 return years. We obtained counts of adult fish at dams for the composite wild/hatchery stocks from the DART web site: http://www.cqs.washington.edu/dart/adult.html). For the natural-origin Snake River fall chinook run, we used updated (unpublished) adult escapements for return years 2000 to 2002 over Lower Granite Dam developed by NWFSC scientists for TAC (memo from Norma Jean Sands to Peter Dygert and Cindy Lefleur, dated 1 December 2003) and adult returns from 1991-1999 from unpublished data submitted to the Biological Review Team for chinook salmon. We then compared the difference in median returns for adult fish between the two periods to the difference in median SARs for Snake River spring-summer chinook salmon for those same periods.

Results

Snake River spring-summer chinook salmon

Estimated SARs (catch + escapement) of Snake River wild spring-summer chinook salmon from the 1999 and 2000 outmigrations increased to levels only previously observed prior to construction of the final mainstem dams in the FCRPS (Fig. 2). The median SAR of 3.0 % (range 1.6 to 3.8 %) from the 1998 to 2000 outmigrations was similar to the median SAR of 3.1% (range 1.9 to 4.6 %) from the 1964-1970 outmigrations based on data from Petrosky et al. (2001), and 81% of the median 3.7 % SAR (range 3.3 to 6.1 %) for the same years based on Raymond's (1988) analyses. The median SAR of 3.0 % was 5 times higher than the median SAR of 0.6 % (range 0.20 to 1.9) from the previous 10 years (1988 to 1997 outmigrations). From the low-flow 2001 outmigration, the SAR presently stands at ca. 1.6%, with 3-ocean fish still returning in the spring-summer of 2004. This return rate already exceeds total SARs for all Snake River wild spring-summer chinook outmigrations between 1976 and 1997.

Snake River fall chinook salmon

The median estimated SAR for natural origin fall chinook between 2000 to 2002 increased 3.4 times over the median adult return for the period 1991-1999 (Fig. 3).

Upper Columbia River spring chinook salmon

As with historic data, the response of stocks of spring chinook salmon in the Upper Columbia River increased, but to a greater degree than did wild Snake River spring-summer chinook salmon (Fig. 3).

Wild steelhead above Bonneville Dam

Median counts of wild upper river summer steelhead at Bonneville Dam increased 4.3 times, from 33 k (range 24 to 58 k) to 143 k (range 112 to 149 k) (Fig. 3.) We have no information on counts of wild steelhead into the Upper Columbia River.

Wild Snake River steelhead

A plot of the trend over time indicates that SARs for Snake River steelhead have increased considerably in the last 2 years compared to the previous 10 (Fig. 4), to levels not observed since the early 1970s and middle 1980s.

Snake River sockeye salmon

We have little to no information about Snake River sockeye salmon. We see few juveniles at dams and nearly no adults have returned for the last decade, the latter in spite of efforts to raise fish in conservation hatcheries to increase numbers of juveniles in the outmigration. Efforts to improve survival of Snake River chinook salmon and steelhead have not benefitted Snake River sockeye salmon to the same degree.

Discussion

By any measure, Snake River spring-summer chinook abundance has increased dramatically in the last few years. We believe this is largely due to a shift in ocean conditions, and that variability in ocean conditions is likely the most important driver of temporal patterns of abundance. However, the relative role of the hydropower system in overall stock performance is still uncertain. We do believe that improvements made to the hydropower system over the last three decades were crucial for preventing even more drastic declines during the recent period of poor ocean conditions and that affects of the hydropower system are likely more important during poor ocean conditions. Unfortunately, we cannot reliably predict future ocean conditions, and thus we cannot rely on the persistence of good ocean conditions. With predictions of increased global warming in the near future, ocean conditions may actually become worse than any we have yetexperienced. For these reasons, we must continue to assess the affects of the hydropower system in the context of all impacts, including those occurring in both seawater and freshwater habitats.

The high SAR estimates for the unmarked population should not come as a surprise. As outlined in the introduction, they have varied historically (although we only have empirical estimates for Snake River fish since 1964). Williams and Matthews (1995) found that conditions in the hydropower system had improved tremendously from those that initially caused large losses of juvenile migrants (Raymond 1979). Williams et al. (2001) also found that survival of yearling Snake River chinook salmon through the present 8 dams of the mainstem FCRPS recently matched or exceeded those estimated to have occurred when the mainstem FCRPS had only 4 dams. Without actual measures of survival, but under the presumption of success from transportation, Raymond (1988) and Williams (1989) predicted that large returns of Snake River spring-summer chinook salmon could once again occur if ocean conditions improved. Using new modeling tools that predict adult returns based on ocean conditions juveniles encountered during their first several months at sea, recent analyses by Scheuerell and Williams (In review) have found that ocean conditions have a high correlation ($R^2 = 0.71$) with SARS of wild Snake River spring-summer chinook salmon (see DISCUSSION section below for details on Large Scale Processes). Based on recent research by Peterson and Schwing (2003), ocean conditions improved dramatically in 1999. We do not know how long these improved conditions will last, but we do at this time predict good adult returns from the juvenile outmigrations through 2003 (with adults returning through 2006) (Scheuerell and Williams In review). Already, based on returns in the last decade, the population growth rate [ln(brood year $_{N\text{ = escapement over upper dam of the current brood year}}$ /brood year $_{N-1}$)] has exceeded 1.0 for 4 consecutive years (the longest stretch since records began in the 1960s) (Fig. 5.)

As with yearling chinook salmon, the estimated adult returns of natural origin fall chinook salmon to above Lower Granite Dam have increased more than 3.5-times greater than levels from outmigrations in the early to mid-1990s. Total numbers of fall chinook salmon over Lower

Granite have also increased tremendously, but much of this increase resulted from large releases of Lyons Ferry Hatchery fish above the dam. Total numbers of natural origin fish above Lower Granite dam in recent years have exceeded all levels observed since the completion of the dam in 1975. The two periods are not directly comparable, however, as harvest rates on fall chinook have changed substantially in recent years with listing of Snake River fall chinook and increased releases of unmarked hatchery fall chinook salmon above Lower Granite Dam.

Steelhead SARs haven't followed the same patterns as yearling chinook salmon SARs. Ocean conditions appear to have affected steelhead differently, although they have had an affect. The very steep decline in steelhead SARs in the early 1990s also occurred for British Columbia stocks and was attributed to changed ocean conditions (Welch et al. 2000). The low spawning populations in the 1990s (some the lowest in the last 35 years) produced comparatively low numbers of wild smolts compared to the 1960s. Thus, even with the recent large increases in adult returns, total adult returns of wild steelhead remain at only approximately one-half the level of the 1960s.

Based On PIT-tagged Fish

Methods

We estimated annual SARs for PIT-tagged Snake River fish based on a Lower Granite Dam equivalent for smolts and adult returns to Lower Granite Dam by following the methods in Sandford and Smith (2002). We estimated how many fish passed the dam on each day of the migration season and totaled the daily estimates. To get each day's estimate, we used the following process:

1) For fish detected on a given day at Little Goose Dam that had previously been detected at Lower Granite Dam, tabulate according to their detection (passage) day at Lower Granite Dam;

2) For fish detected on the same day at Little Goose Dam that had NOT previously been detected at Lower Granite Dam, assign them to their estimated "non-detection passage day" at Lower Granite Dam, assuming that their distribution over days at Lower Granite Dam was proportionate to that of fish detected at Lower Granite Dam;

3) Repeat this process for all days of detection at Little Goose Dam;

4) Sum all these detected and non-detected fish for a given day at Lower Granite Dam;

5) Estimate that day's detection probability by calculating the proportion of detected fish to the total of detected and non-detected fish (after making an adjustment for fish transported at Lower Granite Dam); and

6) Divide the total detected number at Lower Granite Dam on that day (bypassed and transported) by the estimated detection probability to get an estimated daily total.

Formally, this process is referred to as the Schaefer method. We modified the method slightly for estimates in the tails of the passage distribution where the above process wasn't applicable (e.g., for days when no detections occurred at Little Goose Dam)

We then estimated SARs for various "detection-history categories", in particular for fish transported from Lower Granite, Little Goose, Lower Monumental, or McNary Dams, for fish bypassed back to the river one or more times at these dams, and for fish never detected at these dams. (Results and discussion of SARs for multiple-bypassed fish is contained in the "Latent Mortality section below". To do this, we developed daily passage estimates at Lower Granite Dam using the following process:

1) We estimated for each daily Lower Granite passage group the probabilities of detection at Little Goose, Lower Monumental, and McNary Dams using the Cormack-Jolly-Seber survival model (Cormack 1964; Jolly 1965; Seber 1965).

2) We multiplied the estimated daily Lower Granite Dam total by the appropriate detection and transport probabilities. For example, for the detection-history category "not detected at Little Goose Dam and then transported from Lower Monumental Dam", this is equivalent to multiplying the Lower Granite Dam daily estimate by (1 - probability of Little Goose Dam detection) times (probability of Lower Monumental detection).

3) We summed the estimates for all daily groups to get total smolts in each detection-history category.

Next we calculated SARs. For a given detection-history category, this was the ratio of the observed number of adults in the category to the estimated number of smolts in that category. We also estimated the precision for the estimated SAR using bootstrap methods where the individual fish information (i.e., detection history, detection dates, and adult return record) and the entire estimation process were bootstrapped 1,000 times. Confidence limits were generated from the bootstrapped estimates.

Finally, we weighted SARs of PIT-tagged fish by the estimated percentage for the detection history of the untagged population. Since the untagged population of fish passing through the bypass systems at Lower Granite, Little Goose, and Lower Monumental Dams were transported, we used the estimated percentage of first time detections of PIT-tagged fish at those dams to weight the SAR for transported fish at those dams. We combined these SARs with the estimated SARs for fish not detected at collector dams (including McNary Dam) plus the SARs of fish bypassed at McNary Dam to derive a weighted SAR for the total population based on SARs of PIT-tagged fish.

Results

Snake River spring-summer chinook salmon

The overall estimated SARs for wild and hatchery spring-summer chinook salmon (Lower Granite Dam to Lower Granite Dam - not adjusted for harvest) based on weighting SARs of PIT-tagged fish by migration histories of the untagged population ranged from 0.1 to 2.3% (Fig. 6).

Estimated annual SARs for PIT-tagged chinook salmon marked above Lower Granite Dam with different detection histories as juveniles varied widely between years and dams for the 1993 to 2000 outmigrations (Table 2). Most estimates had wide 95% confidence bounds (Table 3). When confidence bounds between two different groups did not overlap, it indicated a significant difference in SARs between the two groups. Thus, no significant differences existed for any comparison groups of wild spring-summer chinook salmon. For hatchery spring-summer chinook salmon, the annual SAR for fish transported from Lower Granite Dam was significantly higher than for in-river migrants (non-detected category) fish from migration years 1997 - 2000.

Table 2. Annual SARs (with total adult returns) for spring-summer chinook salmon PIT-tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population. Abbreviations. LGR = Lower Granite Dam, LGO = Little Goose Dam, LMO = Lower Monumental Dam, MCN = McNary Dam. Bolded groups had significantly different adult return rates.

	Rearing	Transported from (first time det.):				Non-
Year	type	LGR	LGS	LMN	MCN	detected
1993	Wild	0.10 (2)	0.34 (1)	-	-	
	Hatchery	0.09 (4)	-	-	-	0.06 (2)
1994	Wild	0.74 (8)	0.93 (4)	0.18 (1)	-	0.05 (1)
	Hatchery	0.11 (2)	0.12 (1)	0.11 (1)	0.02 (2)	0.09 (7)
1995	Wild	0.39 (7)	0.29 (1)	-	-NA-	0.47 (9)
	Hatchery	0.59 (14)	0.80 (5)	0.37 (1)	-NA-	0.45 (27)
1996	Wild	0.35 (1)	1.10 (1)	-	-	0.20 (4)
	Hatchery	0.30 (6)	-	-	-	0.17 (29)
1997	Wild	0.99 (2)	6.45 (2)	-	-NA-	1.63 (14)
	Hatchery	**0.89 (226)**	0.69 (5)	0.66 (22)	-NA-	**0.67 (162)**
1998	Wild	1.30 (11)	0.89 (3)	0.96 (1)	-NA-	1.43 (31)
	Hatchery	**1.74 (812)**	0.84 (66)	0.57 (7)	-NA-	**1.26 (260)**
1999	Wild	2.59 (32)	2.15 (9)	1.75 (7)	-NA-	2.08 (73)
	Hatchery	**2.75 (697)**	2.91 (481)	1.24 (25)	-NA-	**1.83 (567)**
2000	Wild	1.07 (4)	1.94 (6)	1.00 (2)	-NA-	2.03 (116)
	Hatchery	**3.08 (1029)**	2.18 (310)	1.76 (86)	-NA-	**1.66 (753)**

Table 3. Confidence intervals (95%) around annual SARs (see Table 2) for chinook salmon PIT-tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population. Abbreviations. LGR = Lower Granite Dam, LGO = Little Goose Dam, LMO = Lower Monumental Dam, MCN = McNary Dam.

	Rearing	Transported from (first time det.):				Non-
Year	type	LGR	LGS	LMN	MCN	detected
1993	Wild	0.00 - 0.19	0.00 - 1.01	-	-	-
	Hatchery	0.02 - 0.17	-	-	-	0.00 - 0.17
1994	Wild	0.36 - 1.12	0.19 - 1.58	0.00 - 0.61	-	0.05 - 0.43
	Hatchery	0.00 - 0.27	0.00 - 0.34	0.00 - 0.23	0.00 - 0.03	0.04 - 0.18
1995	Wild	0.22 - 0.62	0.00 - 0.61	-	-NA-	0.20 - 0.58
	Hatchery	0.30 - 0.83	0.33 - 1.38	0.00 - 0.86	-NA-	0.30 - 0.59
1996	Wild	0.00 - 1.43	0.00 - 3.72	-	-NA-	0.00 - 0.46
	Hatchery	0.20 - 0.44	-	-	-NA-	0.12 - 0.21
1997	Wild	0.00 - 2.22	0.00 - 24.2	-	-NA-	0.81 - 2.64
	Hatchery	0.80 - 0.96	0.31 - 1.12	0.00 - 1.35	-NA-	0.60 - 0.74
1998	Wild	0.72 - 2.31	0.28 - 1.58	0.00 - 3.13	-NA-	1.08 - 1.75
	Hatchery	1.66 - 1.81	0.70 - 0.97	0.32 - 0.81	-NA-	1.16 - 1.36
1999	Wild	1.66 - 3.27	0.71 - 3.38	0.93 - 2.80	-NA-	1.73 - 2.36
	Hatchery	2.56 - 2.95	2.62 - 3.09	0.85 - 1.66	-NA-	1.62 - 1.92
2000	Wild	0.25 - 1.91	0.81 - 3.41	0.00 - 1.81	-NA-	1.80 - 2.48
	Hatchery	2.92 - 3.25	1.86 - 2.42	1.31 - 2.31	-NA-	1.40 - 1.71

Snake River steelhead

The overall estimated SARs for wild and hatchery steelhead (Lower Granite Dam to Lower Granite Dam - not adjusted for harvest) based on weighting SARs of PIT-tagged fish by juvenile migration histories of the untagged population ranged from 0.3 to 3.1% (Fig. 7).

Estimated annual SARs for PIT-tagged steelhead marked above Lower Granite Dam with detection histories as juveniles equivalent to the unmarked population varied widely between years and dams for the 1993 to 2000 outmigrations (Table 4). Most estimates had wide 95% confidence bounds (Table 5).

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Table 4. Annual SARs (with total adult returns) for steelhead PIT-tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population. Abbreviations. LGR = Lower Granite Dam, LGO = Little Goose Dam, LMO = Lower Monumental Dam, MCN = McNary Dam. Bolded groups had significantly different adult return rates.

Year	Species	Rearing type	Transported from (first time det.): LGR	LGS	LMN	MCN	Non-detected
1993	Steelhead	Wild	0.24 (2)	-	-	1.85 (1)	-
		Hatchery	0.05 (1)	0.59 (1)	0.59 (2)	-	0.35 (2)
1994	Steelhead	Wild	1.70 (6)	0.46 (1)	0.52 (1)	-	0.93 (6)
		Hatchery	**1.08 (21)**	-	0.41 (2)	0.07 (1)	**0.10 (7)**
1995	Steelhead	Wild	-	-	4.17 (1)	-NA-	-
		Hatchery	0.70 (14)	1.60 (5)	-	-NA-	0.90 (11)
1996	Steelhead	Wild	0.99 (1)	-	-	-NA-	0.35 (2)
		Hatchery	0.36 (4)	-	-	-NA-	0.36 (14)
1997	Steelhead	Wild	1.32 (3)	-	-	-NA-	0.22 (1)
		Hatchery	0.60 (10)	-	-	-NA-	0.19 (8)
1998	Steelhead	Wild	0.33 (1)	-	-	-NA-	1.20 (9)
		Hatchery	0.63 (5)	0.24 (1)	0.52 (1)	-NA-	0.93 (24)
1999	Steelhead	Wild	2.49 (6)	4.21 (4)	2.53 (2)	-NA-	2.68 (25)
		Hatchery	0.95 (8)	1.20 (4)	-	-NA-	1.43 (37)
2000	Steelhead	Wild	2.82 (7)	3.08 (4)	2.11 (3)	-NA-	1.78 (36)
		Hatchery	**3.04 (14)**	0.98 (1)	0.61 (1)	-NA-	**0.97 (39)**

Table 5. Confidence intervals (95%) around annual SARs (see Table 4) for steelhead PIT-tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population. Abbreviations. LGR = Lower Granite Dam, LGO = Little Goose Dam, LMO = Lower Monumental Dam, MCN = McNary Dam

Year	Rearing type	Transported from (first time det.): LGR	LGS	LMN	MCN	Non-detected
1993	Wild	0.00 - 1.67	1.30 - 5.12	0.00 - 2.68	-NA-	0.42 - 1.25
	Hatchery	0.00 - 0.15	0.00 - 1.84	0.00 - 1.72	-	0.00 - 0.99
1994	Wild	0.29 - 2.91	0.00 - 1.69	0.00 - 1.26	-	0.28 - 1.95
	Hatchery	0.68 - 1.52	-	0.00 - 0.89	0.00 - 0.14	0.04 - 0.15
1995	Wild	-	-	0.00 - 11.7	-NA-	0.00 - 1.22
	Hatchery	0.39 - 1.25	0.62 - 3.15	-	-NA-	0.50 - 1.23
1996	Wild	0.00 - 3.96	-	-	-NA-	0.00 - 1.04
	Hatchery	0.17 - 0.57	-	-	-NA-	0.17 - 0.53
1997	Wild	0.00 - 2.59	-	-	-NA-	0.00 - 0.55
	Hatchery	0.23 - 1.08	-	-	-NA-	0.07 - 0.28
1998	Wild	0.00 - 1.01	-	-	-NA-	0.56 - 1.94
	Hatchery	0.14 - 1.25	0.00 - 0.70	0.00 - 1.64	-NA-	0.65 - 1.22
1999	Wild	0.81 - 4.48	1.07 - 9.01	0.00 - 8.11	-NA-	1.06 - 2.20
	Hatchery	0.49 - 1.64	0.59 - 2.00	-	-NA-	1.08 - 1.86
2000	Wild	0.46 - 5.88	0.79 - 4.61	0.00 - 4.93	-NA-	1.30 - 2.31
	Hatchery	1.54 - 4.61	0.00 - 2.76	0.00 - 2.59	-NA-	0.60 - 1.34

Discussion

For spring-summer chinook salmon, few treatments from any year attained SARs that met the 2 to 6% SAR range deemed necessary for recovery of the listed stocks while allowing for historic harvest rates (Table 2). In contrast, our estimated SAR for the wild population based on total wild returns to Lower Granite Dam divided by the estimated number of wild juveniles producing the adult returns for the same years exceeded 2.5% in 1999 and 2000 (Fig. 6). Estimates of differences in SARs based on PIT-tagged fish versus the non-tagged population showed no clear trend in the early years, but this may have resulted from estimating SARs from small numbers of adult returns. For wild fish, when total adult returns increased to over 200 fish beginning in 1998, the estimated SAR based on PIT-tagged fish was clearly lower than the estimate for the untagged population. We observed the same trends for wild steelhead. In all years, the estimated return rate for the untagged population exceeded the return rate of PIT-tagged fish (Fig. 7).

These results suggest that SARs for PIT-tagged wild fish do not represent the total SAR for the unmarked population. Thus, we conclude that although PIT-tagged wild chinook salmon and steelhead provide useful data when assessing the difference in return rates of different treatment groups, they do not apparently represent SARs for the wild populations. On-the-other hand, we saw no evidence that PIT-tagged hatchery chinook salmon systematically underestimated the SARs of the untagged population of hatchery chinook salmon. We don't have any SAR estimates for the unmarked population of hatchery steelhead to compare to PIT-tagged fish. We do urge caution, however, when using absolute return rates of hatchery PIT-tagged fish to make inferences about the total untagged population as hatchery fish in the Snake River basin do not receive PIT tags in proportion to the total hatchery population. Thus, a bias in PIT-tagged derived SARs based on hatchery fish will likely exist.

TRANSPORTATION EVALUATIONS

Methods

General

We evaluated the efficacy of transportation two ways. First, we compared the return rate of transported fish to the return rate of control fish that migrated volitionally through the hydropower system. This provided a *T:I* ratio, simply the ratio of the return rates of transported (*T*) fish and in-river migrants (*I*). We also evaluated D, defined as the ratio of post-Bonneville Dam survival for transported fish to that of the in-river migrants. We provide details of the methodology below.

We based our evaluation of transportation on comparisons of return rates from fish PIT-tagged as juveniles that migrated through the hydropower system versus fish collected and transported. We based most of our evaluations on fish from two general sources. We utilized fish PIT-tagged for the CSS above Lower Granite Dam that passed through sort-by-code systems installed in bypass systems at collector dams (Lower Granite, Little Goose, and Lower Monumental Dams on the Snake River and McNary Dam on the Columbia River) and were specifically released to evaluate transportation. Of the fish collected, some were automatically diverted to raceways for transportation, while others were returned to the river to allow estimation of survival for the downstream migrants. We also PIT-tagged juvenile fish collected at Lower Granite Dam, some of which we released into raceways for subsequent transportation and others we released to the tailrace of the dam. Finally, as slide gates are not 100% effective at diverting

PIT-tagged fish back to the river, some non-designated fish PIT-tagged above Lower Granite Dam get transported. We evaluated these fish where possible, but due to quite small sample sizes, SARs for these have large confidence bounds.

Groups of fish PIT tagged above and at Lower Granite Dam each have advantages and disadvantages for evaluating transportation. For fish PIT tagged above the dam, fish collected at Lower Granite Dam presumably represent the untagged population collected at the dam, while fish not collected (therefore not detected) represent the unmarked population of fish that passed the dam through turbines and spill. However, for fish tagged above the dam, we do not have a direct measure of how many non-detected fish pass the dam (we can estimate this). Moreover, when an adult returns that was not detected as a juvenile, we do not know when the fish passed the dam as a juvenile. For groups of these fish, we can only estimate annual transport to in-river ratios (*T/I*) and annual values of D. For fish PIT tagged at Lower Granite Dam, no "true" controls exist because all fish for studies are first collected from the juvenile bypass facilities at Lower Granite Dam. Thus, no sample exists that represents untagged, uncollected fish. However, tagging at dams has some advantages. After release, we know the number of downstream migrants that subsequently represent the untagged population. Further we can estimate temporal SAR trends for transported and in-river migrants. From this we can estimate temporal D trends.

Studies specifically designed to evaluate transportation of Snake River fall chinook salmon only began in 2001. However, as PIT-tag systems do not effectively bypass 100% of PIT-tagged fish back to the river, each year a relatively small number of PIT-tagged fish arriving at Lower Granite, Little Goose, Lower Monumental, and McNary Dams did get transported. In 1995, we began PIT tagging and releasing Lyons Ferry hatchery fall chinook salmon in the Clearwater and free-flowing Snake River above Lewiston to evaluate survival. We estimated SARs for the combined group of fish transported from any of the collector dams and compared them to SARs of the combined fish bypassed only once at each of the dams. We also conducted separate analyses for fish detected prior to 1 September and fish detected on 1 September or later. We further developed ratios of the combined transported fish for each year to the combined bypassed fish for each year and developed 95% confidence bounds for the ratios.

We used data from studies in 1995 and 1996 to evaluate the efficacy of transportation at McNary Dam (after construction of the new juvenile bypass/collection facilities in 1994). In those 2 years, approximately 110,000 and 120,000 juvenile subyearling chinook salmon, respectively, were collected in the juvenile bypass facility at the dam and coded-wire tagged (CWT). Fish were tagged 5 days/week in proportion to the daily collection. Each day approximately 60% of the fish were released to the tailrace of the dam through the bypass facility pipe. The other 40% of the fish were transferred into barges and released downstream of Bonneville Dam. Evaluations to compare returns of transported fish compared to those released to the tailrace of McNary Dam were based on CWT recoveries from fisheries and hatcheries.

Computing D (PATH Method)

The PATH (Marmorek et al. 1998a) definition of D (c.f. PATH Preliminary Decision Analysis Report on Snake River Spring/Summer Chinook; Figure 4.2-1 caption) involves terms for "direct survival" of in-river migrants and "direct survival" of transported juvenile fish. This requires estimation of the number of fish in each group (transported or in-river migrants) that were alive in the river below Bonneville Dam. The counted number of adult returns to Lower Granite Dam in each group is divided by the estimated number of juveniles below Bonneville to estimate post-Bonneville survival. The estimate of D is calculated as the ratio of post-Bonneville survival for the transported group to post-Bonneville survival for the in-river migrant's group.

For a given dam, the expected return rates (SARs) for transported and in-river migrants are each composed of two components: the expected survival probability from the dam to below Bonneville Dam, and the expected survival probability from below Bonneville Dam to adult return. The SARs can be described by the equations

$$SAR_T = S_T \cdot \lambda_T$$

and

$$SAR_I = S_I \cdot \lambda_I$$

where the subscripts *T* and *I* refer to transported and in-river migrants, respectively; *S* is the downstream survival component, and λ is the post-Bonneville Dam component. The ratio of the SARs is the familiar *T:I* ratio:

$$T{:}I = \frac{SAR_T}{SAR_I} = \frac{S_T}{S_I} \cdot \frac{\lambda_T}{\lambda_I} = \frac{S_T}{S_I} \cdot D$$

This equation decomposes the *T:I* ratio into downstream and post-Bonneville Dam components, and introduces the parameter *D*, which is the ratio of post-Bonneville Dam survival for transported fish to that for in-river migrants. If transported fish and in-river migrants have the same survival probability from the transport release site to return as adults, then D=1.0. If transported fish incur greater mortality after release from the barge, then D<1.0.

Transportation benefits fish stocks from a particular location only if the expected SAR for transported fish exceeds that for in-river migrants; that is, if the *T:I* ratio is expected to exceed 1.0. Because S_T (survival in the barge from the collection dam to below Bonneville Dam) is near 1.0, the decision reduces to comparing survival to below Bonneville for fish left in the river versus differential post-Bonneville Dam survival. In terms of the equations, transportation benefits fish only if $D > S_I$.

One consequence of this relationship is that if *D* is the same for each transportation site, then the benefit of transportation is greater for collection sites farther upstream. This is because S_I increases for sites farther downstream. In other words, fish transported from Lower Granite Dam avoid the higher direct mortality incurred by fish prior to their collection and transportation from McNary Dam. The value of D may depend on the collection site, thus we apply a separate value for each collection site. We did not make a survival estimate from above Lower Granite Dam to the Lower Granite Dam tailrace, as both in-river migrants and transported juveniles transited the same area in common, and thus, any value cancels out of calculations without any effect on estimated D.

The estimated number of in-river migrants (control group) alive below Bonneville Dam is derived by multiplying the annual estimate of the number of "control" fish arriving at Lower Granite Dam by the estimated annual average survival between Lower Granite and Bonneville Dam tailrace. With the PATH definition, it is impossible to calculate date-specific differential survival between transported fish and the "true" control group within a single migration season. While we can estimate the number of juveniles in the "never-detected" category that passed Lower Granite Dam on any particular day, we have no way of knowing what day a returning adult in that category passed Lower Granite Dam as a juvenile. Thus, we can't calculate the SAR for the never-detected group for a specific date.

We also tabulated early returns from subyearling chinook salmon PIT tagged at McNary Dam in 2001 and 2002 to evaluate transportation. We do not have complete returns (probably less than 60% for the 2001 fish and less than 30% of the 2002 fish. We only graphed results groups of fish tagged on a weekly basis to observed how the early returns compared to studies in 1995 and 1996.

Computing D (Non-PATH)

We also evaluated data to determine how differential post-Bonneville survival between transported and in-river migrants might change throughout a single migration season. As identified above, we used fish marked at Lower Granite Dam and compared transported fish to those released into the tailrace that subsequently had the same detection history as the untagged population of fish. We used 6-day blocks for fish marked and released at Lower Granite Dam and compared SARs for those transported within each block to those released to the tailrace of the dam that subsequently had the detection history of unmarked fish in the population. For studies in 2000, the transport groups were developed from fish collected at Little Goose Dam. We used the same methods to determine temporal D values as we did to determine average D over the season.

Results

Annual estimates of SARs for transported and in-river migrants

Based on Sandford and Smith (2002) methodologies applied to fish PIT-tagged above Lower Granite Dam from 1993 through 2003, we estimated that the combined annual percentage of the non-tagged chinook salmon population transported from Lower Granite, Little Goose, Lower Monumental, and McNary Dams ranged from approximately 62% to nearly 100% (Table 6).

Table 6. Combined annual percentage of the non-tagged yearling chinook salmon population transported from Lower Granite, Little Goose, Lower Monumental, and McNary Dams.

Year	Wild chinook	Hatchery chinook
1993	88.5	88.1
1994	87.7	84.0
1995	86.4	79.6
1996	71.0	68.7
1997	71.1	71.5
1998	82.5	81.4
1999	85.9	77.3
2000	70.4	61.9
2001	99.0	97.3
2002	72.1	64.2
2003	70.4	61.5

Clearly, the ultimate effect of the FCRPS on yearling chinook salmon from the Snake River basin depends to a large degree on the efficacy of fish transportation.

Estimated annual SARs for PIT-tagged and transported chinook salmon marked above Lower Granite Dam during outmigration years 1993 to 2000 varied widely between years and dams (Table 2), as did the 95% confidence bounds (Table 3). For hatchery spring-summer chinook salmon, the annual SAR for fish transported from Lower Granite Dam was significantly higher than for in-river migrants (non-detected category) from migration years 1997 to 2000.

Annual SARs for PIT-tagged juvenile spring-summer chinook salmon marked at Lower Granite Dam during outmigration years 1995 to 2000 varied widely between years and at sites (Table 7). The fish included in these results were first-time detections at the respective dam. For fish marked at Lower Granite Dam, first time detection was defined as after release from Lower

Granite Dam (non-detected fish represented the route of passage of the non-tagged population downstream of Lower Granite Dam). Annual adult returns for wild spring-summer chinook salmon collected and marked at Lower Granite Dam were high enough that sufficiently narrow confidence bounds existed to indicate significantly higher annual SARs for transported fish in 1995 and 1999, but not in 1996, 1998, and 2000 (Table 8).

Table 7. Annual SARs (with total adult returns) for spring-summer chinook salmon PIT-tagged at Lower Granite Dam for transportation studies between 1995 and 2000, compared to annual SARs of non-detected fish (fish that represent the migration history for the non-tagged population).

	Rearing	Transported from:				Non-
Year	type	LGR	LGS	LMN	MCN	detected
1995	Wild	0.38 (92)	0.24 (8)	0.28 (4)	-	0.23 (26)
	Hatchery	0.54 (450)	0.37 (17)	0.30 (5)	-	0.32 (123)
1996	Wild	0.11 (9)	-	-	-	0.06 (3)
	Hatchery	0.13 (47)	0.10 (1)	-	-	0.11 (27)
1997			No studies			
1998	Wild	0.60 (34)	-	-	-NA-	0.95 (28)
	Hatchery	0.62 (245)	0.32 (6)	0.19 (2)	-NA-	0.57 (134)
1999	Wild	2.10 (176)	0.70 (1)	2.41 (15)	-NA-	1.35 (26)
	Hatchery	1.97 (833)	2.09 (12)	1.47 (50)	-NA-	1.45 (242)
2000[a]	Wild	-NA-	1.47 (255)	0.66 (7)	-NA-	1.44 (385)
	Hatchery	-NA-	-NA-	-NA-	-NA-	-NA-

[a] Fish were tagged at Lower Granite Dam, released into tailrace and collected and transported from Little Goose Dam.

Table 8. Confidence intervals (95%) around annual SARs (see Table 7) for spring-summer chinook salmon PIT-tagged at Lower Granite Dam for transportation studies between 1995 and 2000, compared to intervals around annual SARs of non-detected fish (fish that represent the migration history for the non-tagged population).

Year	Rearing type	Transported from: LGR	LGS	LMN	MCN	Non-detected
1995	Wild	0.30 - 0.45	0.17 - 0.59	0.07 - 0.49	-	0.17 - 0.28
	Hatchery	0.51 - 0.57	0.26 - 0.49	0.13 - 0.50	-	0.28 - 0.36
1996	Wild	0.05 - 0.18	-	-	-	0.02 - 0.15
	Hatchery	0.10 - 0.17	0.00 - 0.21	-	-	0.07 - 0.14
1997			No studies			
1998	Wild	0.46 - 0.77	-	-	-NA-	0.61 - 1.28
	Hatchery	0.58 - 0.68	0.16 - 0.55	0.00 - 0.38	-NA-	0.48 - 0.65
1999	Wild	1.83 - 2.42	0.00 - 2.99	1.51 - 4.00	-NA-	0.94 - 1.80
	Hatchery	1.90 - 2.06	1.05 - 3.25	1.29 - 1.71	-NA-	1.32 - 1.60
2000[a]	Wild	-NA-	1.36 - 1.57	0.39 - 0.95	-NA-	1.36 - 1.57
	Hatchery	-NA-	-NA-	-NA-	-NA-	-NA-

[a] Fish were tagged at Lower Granite Dam, released into tailrace and collected and transported from Little Goose Dam.

Annual Estimates of Differential Post-Bonneville Dam Survival (D): Transport Location-Specific and Overall

Annual estimates provide a general description of differences in return rates between transported and in-river migrants, and differences between transport locations.

Large adult returns in recent years have generally improved our ability to estimate differential post-Bonneville Dam survival separately for each transportation dam, and greatly increased the precision on the overall estimate. In all comparisons of hatchery and wild Snake River spring-summer chinook salmon, the greatest number of returning PIT-tagged adults came from the 1999 and 2000 outmigrations (Tables 9 and 10).

No apparent consistent results exist. To summarize results, we offer the following, sometimes tentative, observations and conclusions:

(1) For wild and hatchery fish, the geometric mean annual estimated D from migration years 1994 through 2000 ranged between 0.55 and 0.61. That is, averaged over years and throughout migration seasons, survival for transported fish from below Bonneville Dam as a juvenile to

return as an adult has averaged less than two-thirds that of the in-river migrants that arrived below Bonneville Dam.

(2) Wild and hatchery spring-chinook salmon transported from Lower Monumental Dam have had the lowest average post-Bonneville Dam survival. Average in-river survival from Lower Monumental Dam to Bonneville Dam has exceeded this average "D", indicating that fish not transported from Lower Monumental Dam had higher average annual SARs than fish transported from the site.

(3) For wild spring-summer chinook salmon, average post-Bonneville Dam survival for fish transported from Lower Granite Dam has roughly equaled the average survival of in-river migrants that migrated between Lower Granite and Bonneville Dams. Wild chinook salmon transported from Lower Granite Dam in 2000 had particularly low annual post-Bonneville Dam survival.

(4) For hatchery spring-summer chinook salmon, average post-Bonneville Dam survival for fish transported from Lower Granite Dam has considerably exceeded the average estimated survival for the in-river migrants that migrated between Lower Granite and Bonneville Dams.

(5) Small sample sizes resulted in imprecise annual D estimates. For example, even with more than 2,000 returns of hatchery chinook salmon in 2000, a wide 95% confidence interval still existed (Table 10). The number of juvenile fish from the outmigration, however, provided the ability to make a relative precise estimate for survival for in-river migrants that migrated between Lower Granite and Bonneville Dams.

Table 9. Annual estimates of differential post-Bonneville survival (D) for Snake River wild spring-summer chinook salmon transported from various dams and for weighted average from all sites. Total adult returns are provided in parentheses (when 0 adults in a category, the number of juveniles is given as well). PIT-tagged in-river migrants represent passage histories most representative of non-tagged fish that migrated to Bonneville Dam. All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence interval for weighted average given in brackets.

Year	Non-trans-ported	Transported all sites	Transported LGR	Transported LGO	Transported LMO
1994	(6)	0.683 (13) [0.254, 1.844]	0.770 (8)	1.187 (4)	0.239 (1)
1995	(10)	0.457 (8) [0.177, 1.184]	0.559 (7)	0.467 (1)	(0/195)
1996	(5)	1.081 (2) [0.202, 5.783]	0.688 (1)	2.453 (1)	(0/43)
1997	(17)	0.498 (4) [0.162, 1.539]	0.224 (2)	1.262 (2)	(0/14)
1998	(48)	0.430 (15) [0.238, 0.783]	0.480 (11)	0.334 (3)	0.421 (1)
1999	(104)	0.656 (48) [0.460, 0.934]	0.730 (32)	0.641 (9)	0.563 (7)
2000	(174)	0.336 (12) [0.184, 0.613]	0.245 (4)	0.474 (6)	0.274 (2)
		geometric mean: 0.553	**0.478**	**0.779**	**0.353**

Table 10. Annual estimates of differential post-Bonneville survival (D) for Snake River hatchery spring-summer chinook salmon transported from various dams and for weighted average from all sites. Total adult returns are provided in parentheses (when 0 adults in a category, the number of juveniles is given as well). Controls are PIT-tagged fish with passage histories most representative of nontagged fish that migrated to Bonneville Dam in-river (control adults given in parentheses next to year label). All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence interval for weighted average given in brackets.

Year	Non-trans-ported	Transported all sites			Transported LGR		Transported LGO		Transported LMO	
1994	(7)	0.316	(6)	[0.104, 0.963]	0.314	(2)	0.445	(1)	0.468	(1)
1995	(32)	0.886	(20)	[0.501, 1.572]	0.808	(14)	1.238	(5)	0.661	(1)
1996	(32)	0.409	(6)	[0.168, 0.995]	0.780	(6)		(0/510)		(0/366)
1997	(185)	0.523	(233)	[0.430, 0.639]	0.561	(226)	0.469	(5)	0.517	(2)
1998	(336)	0.638	(885)	[0.561, 0.727]	0.829	(812)	0.405	(66)	0.319	(7)
1999	(736)	0.903	(1203)	[0.821, 0.993]	0.930	(697)	1.036	(481)	0.477	(25)
2000	(915)	0.870	(1426)	[0.798, 0.948]	0.961	(1030)	0.726	(310)	0.658	(86)
		geometric mean: 0.606			**0.700**		**0.654**		**0.502**	

* 2 fish transported from McNary Dam returned as adults; estimated differential post-Bonneville Dam survival for McNary transport = 0.098.

Within season variability in transportation and D

For fish PIT-tagged at Lower Granite Dam, we have known timing for transported and subsequently non-detected fish. From these fish we determined that not only did SARs vary over the course of the outmigration, but the variation in timing changed between years. Transported chinook salmon had greater temporal changes in SAR than in-river migrants (Figs. 8, 9, 10, and 11.) For wild fish, due to higher variability about SAR estimates, we detected only one significantly higher SAR in one treatment pair (the transported fish in the 12-18 May 2000 period returned at higher rates.) The SARs of hatchery fish had tighter confidence bounds, and thus, we detected more significant differences in treatment pairs. In 1998 and 1999, the earliest non-detected in-river fish migrating below Bonneville Dam returned at significantly higher rates than transported fish; whereas in all years, transported fish returned at significantly higher rates for several pairs of groups during the mid- to latter part of the outmigration.

Adult upstream conversion rates

Based on PIT-tag detections at Bonneville and Lower Granite Dams in 2002 and 2003 of wild 2- and 3-ocean spring-summer chinook salmon adults returning from the 2000 and 2001 outmigrations, transported and in-river fish had nearly the same high adult conversion rates (Table 10a.) These conversion rates were not adjusted for Zone 6 harvest. They far exceed the average values ascribed to the hydropower system used in recent PATH analyses (Marmorek et al. 1998a). As adult fish passage facilities and upstream conditions have changed comparatively little in the past several decades, analyses based on old conversation rates likely contain considerable error.

Table 10a. Conversion rates (number of adult fish detected at Lower Granite dam/number of adult fish detected at Bonneville Dam) for wild adult spring-summer chinook salmon PIT tagged as juveniles at Lower Granite in 2000 and 2001 and either returned to the river or transported.

Year of outmigration	Year of adult return	In-river	Transported
2000	2002	0.86 (196/228)	0.87 (97/111)
	2003	0.82 (324/394)	0.84 (117/140)
2001	2003	NA -----	0.92 (91/99)

Snake River Fall Chinook Salmon

For juvenile fish detected prior to 1 September, in 4 of 6 years, the SAR of the combined bypassed group exceeded the SAR of the combined transported group (Fig. 12). For juvenile fish detected in the late period, transported and bypassed fish each had 2 years when they returned at higher rates than the other (Fig. 13). However, the confidence bounds about the ratios for groups extended from zero (or nearly so) to above 1 (and mostly considerably higher than 1).

Upper Columbia River Subyearling Migrants

In both 1995 and 1996, subyearling chinook salmon transported from McNary Dam generally had higher return rates than in-river migrants when flows at the dam exceeded approximately 6,500 m3/second (approximately 225,000 cfs) and water temperatures remained below 18 ºC (Figs. 14 and 15.) Counter to expectations, these results suggest that transporting subyearling chinook salmon under conditions of higher water temperatures and lower flows decreases adult return rates compared to returning fish to the river. They also contrast to studies in the early 1980s conducted at the old juvenile facility at McNary Dam, where transported fish returned at 2 to 4 times the rate of fish released to the tailrace of the dam. In 2001 and 2002 we PIT-tagged subyearling chinook salmon at McNary Dam for additional transportation evaluations to determine if results from the 1995 and 1996 studies apply under the apparently improved ocean conditions that began in 1999. PRELIMINARY data from these years (1-ocean and 2-ocean returns from 2001 - 62 total fish all treatments; 1-ocean fish from 2002 - 143 total fish all treatments) at this time do not appear to the same as the earlier years (Figs. 16 and 17.)

Snake River Steelhead

Annual estimates of SARs for transported and in-river migrants

Based on Sandford and Smith (2002) methodologies applied to fish PIT-tagged above Lower Granite Dam from 1993 through 2003, we estimated that the combined annual percentage of the non-tagged steelhead population transported from Lower Granite, Little Goose, Lower Monumental, and McNary Dams ranged from approximately 68% to nearly 100% (Table11).

Table 11. Combined annual percentage of the non-tagged yearling chinook salmon population transported from Lower Granite, Little Goose, Lower Monumental, and McNary Dams.

Year	Wild steelhead	Hatchery steelhead
1993	93.2	94.7
1994	91.3	82.2
1995	91.8	94.3
1996	79.8	82.9
1997	87.5	84.5
1998	88.2	87.3
1999	87.6	88.5
2000	83.9	81.5
2001	99.3	96.7
2002	75.2	70.4
2003	72.9	68.4

As with yearling chinook salmon, because of the high proportion of steelhead transported, clearly the ultimate effect of the FCRPS on steelhead from the Snake River basin depends to a high degree on the efficacy of fish transportation.

Estimated annual SARs for steelhead PIT tagged above Lower Granite Dam and transported during outmigration years 1993 to 2000 varied widely between years and dams (Table 4), as did the 95% confidence bounds (Table 5). Adult returns of wild steelhead in most years at any one dam rarely exceeded 5 fish. For hatchery steelhead, the annual SAR for fish transported from Lower Granite Dam was significantly higher than for in-river migrants (non-detected category) in migration years 1994 and 2000.

Annual SARs for PIT-tagged juvenile steelhead marked at Lower Granite Dam during outmigration years 1998 to 2000 varied widely between years, treatments, and sites (Table 12). The fish included in these results were first-time detections at the respective dam. For fish marked at Lower Granite Dam, first time detection was defined as after release from Lower Granite Dam (non-detected fish represented the route of passage of the non-tagged population downstream of Lower Granite Dam). The annual SARs of transported wild and hatchery steelhead were significantly higher for transported fish than in-river migrants from both the 1999 and 2000 outmigration (Table 13). Too few fish returned from marking in 1998 to determine differences in return rates.

Table 12. Annual SARs (with total adult returns) for steelhead PIT-tagged at Lower Granite Dam for transportation studies between 1998 and 2000, compared to annual SARs of non-detected fish (fish that represent the migration history for the non-tagged population).

Year	Rearing type	Transported from: LGR	LGS	LMN	MCN	Non-detected
1998	Wild	-	0.35 (1)	0.72 (3)	-NA-	0.37 (7)
	Hatchery	-	0.71 (7)	0.24 (2)	-NA-	0.41 (24)
1999	Wild	1.42 (86)	0.80 (1)	2.27 (9)	-NA-	0.54 (8)
	Hatchery	1.08 (442)	1.43 (15)	0.99 (22)	-NA-	0.79 (82)
2000	Wild	-NA-	3.96 (979)	4.43 (101)	-NA-	1.85 (435)
	Hatchery	-NA-	1.99 (11)	1.73 (11)	-NA-	0.85 (79)

[a] Fish were tagged at Lower Granite Dam, released into tailrace and collected and transported from Little Goose Dam.

Table 13. Confidence intervals (95%) around annual SARs (see Table 12) for steelhead PIT-tagged at Lower Granite Dam for transportation studies between 1998 and 2000, compared to intervals around annual SARs of non-detected fish (fish that represent the migration history for the non-tagged population).

Year	Rearing type	LGR	Transported from: LGS	LMN	MCN	Non-detected
1998	Wild	-NA-	0.00 - 1.05	0.00 - 1.77	-NA-	0.16 - 0.61
	Hatchery	-NA-	0.10 - 1.36	0.00 - 0.69	-NA-	0.27 - 0.56
1999	Wild	1.19 - 1.70	0.00 - 2.39	1.16 - 3.70	-NA-	0.27 - 0.94
	Hatchery	1.02 - 1.14	1.00 - 1.83	0.78 - 1.19	-NA-	0.63 - 0.92
2000[a]	Wild	-NA-	3.80 - 4.12	3.82 - 5.10	-NA-	1.71 - 1.98
	Hatchery	-NA-	1.01 - 3.37	0.87 - 2.85	-NA-	0.71 - 1.06

[a] Fish were tagged at Lower Granite Dam, released into tailrace and collected and transported from Little Goose Dam.

Annual estimates of differential post-Bonneville Dam survival (D): transport location-specific and overall

Here we summarize data on annual estimates of D for steelhead. Large adult returns in recent years have generally improved our ability to estimate differential post-Bonneville Dam survival separately for each transportation dam, and greatly increased the precision on the overall estimate. For hatchery and wild Snake River steelhead, the greatest number of returning PIT-tagged adults have occurred in 1999 and 2000 (Tables 14 and 15).

Nonetheless, as with yearling chinook salmon, no apparent consistent results exist. To summarize results, we offer the following observations:

(1) For hatchery and wild steelhead, the geometric mean annual estimated D from migration years 1994 through 2000 ranges widely (Tables 14 and 15). Sometimes, survival for transported fish from below Bonneville Dam as a juvenile to return as an adult is lower than the in-river migrants, but at other times higher.

(2) For hatchery steelhead, average post-Bonneville Dam survival for fish transported from Lower Granite Dam has considerably exceeded the average estimated survival for the in-river migrants that migrated between Lower Granite and Bonneville Dams. (Data are not sufficient to judge for wild steelhead).

(3) It is very difficult to estimate annual D values precisely. The number of juvenile fish from the outmigration, however, provided the ability to make a relative precise estimate for survival for in-river migrants that migrated between Lower Granite and Bonneville Dams.

Table 14. Annual estimates of differential post-Bonneville survival (D) for Snake River wild steelhead transported from various dams and for weighted average from all sites. Total adult returns are provided in parentheses (when 0 adults in a category, the number of juveniles is given as well). Controls are PIT-tagged fish with passage histories most representative of nontagged fish that migrated to Bonneville Dam in-river (control adults given in parentheses next to year label). All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence interval for weighted average given in brackets.

Year	Non-trans-ported	Transported all sites	Transported LGR	Transported LGO	Transported LMO
1994	(6)	0.531 (8) [0.178, 1.581]	0.663 (6)	0.211 (1)	0.266 (1)
1995	(1)	0.981 (1) [0.058, 16.710]		(0/66)	10.023 (1)
1996	(5)	0.978 (2) [0.181, 5.279]	0.678 (1)	2.214 (1)	(0/11)
1997	(4)	0.536 (3) [0.115, 2.492]	0.844 (3)	(0/44)	(0/23)
1998	(9)	0.118 (1) [0.014, 0.976]	0.165 (1)	(0/93)	(0/93)
1999	(18)	1.013 (12) [0.475, 2.163]	0.735 (6)	1.343 (4)	0.882 (2)
2000	(41)	0.691 (14) [0.368, 1.296]	0.660 (7)	0.801 (4)	0.613 (3
	geometric mean:	**0.582**	**0.550**	**0.842**	**1.757**

Table 15. Annual estimates of differential post-Bonneville survival (D) for Snake River hatchery steelhead transported from various dams and for weighted average from all sites. Total adult returns are provided in parentheses (when 0 adults in a category, the number of juveniles is given as well). Controls are PIT-tagged fish with passage histories most representative of nontagged fish that migrated to Bonneville Dam in-river (control adults given in parentheses next to year label). All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence interval for weighted average given in brackets.

Year	Non-transported	Transported all sites	Transported LGR	Transported LGO	Transported LMO
1994	(7)	2.707 (23) [1.140, 6.429]	3.684 (20)	(0/1007)	1.943 (2)
1995	(14)	0.435 (19) [0.214, 0.884]	0.392 (14)	0.996 (5)	(0/88)
1996	(17)	0.294 (4) [0.097, 0.896]	0.446 (4)	(0/353)	(0/94)
1997	(8)	0.968 (10) [0.374, 2.505]	1.615 (10)	(0/158)	(0/119)
1998	(26)	0.326 (7) [0.139, 0.767]	0.374 (5)	0.152 (1)	0.373 (1)
1999	(41)	0.332 (12) [0.171, 0.642]	0.336 (8)	0.457 (4)	(0/250)
2000	(41)	1.051 (14) [0.562, 1.967]	1.291 (13)	(0/102)	0.345 (1)
		geometric mean: 0.627	**0.776**	**0.411**	**0.630**

* In 1994, 1 fish transported from McNary Dam returned as an adult; estimated differential post-Bonneville Dam survival for McNary Dam transport = 0.417.

Within season variability in transportation and D

For steelhead PIT-tagged at Lower Granite Dam, we have known timing for transported and subsequently non-detected fish. From these fish we determined that not only did SARs vary over the course of the outmigration, but the variation in timing changed between years. Transported fish had greater temporal changes in SAR than in-river migrants (Figs. 18 and 19). No consistent pattern appeared. The majority of treatment pairs did not have significant differences in adult returns. As with wild spring-summer chinook salmon, it appeared that slightly higher SARs generally existed for the first groups of fish in a season. Likewise, transported fish tended to have greater SARs during the middle of the migration.

Adult upstream conversion rates

Based on PIT-tag detections at Bonneville and Lower Granite Dams between 2001 and 2003 of wild 1- and 2-ocean steelhead adults returning from the 2000 outmigrations, transported fish had lower conversion rates to Lower Granite Dam than did in-river fish (Table 15a.) We know that steelhead transported as juveniles return to the river generally later than in-river migrant juveniles, thus some of the differences in conversion rates may relate to differences in harvest directed at steelhead or incidental to fall chinook harvest. We haven't yet had the opportunity to evaluate this possibility. Another possibility for the difference could relate to higher stray rates for transported fish compared to in-river fish. Again we do not have data at this time to determine this.

Table 15a. Conversion rates (number of adult fish detected at Lower Granite dam/number of adult fish detected at Bonneville Dam) for wild adult steelhead PIT tagged as juveniles at Lower Granite in 2000 and 2001 and either returned to the river or transported.

Year of outmigration	Year of adult return	In-river	Transported
2000	2001	0.83 (347/418)	0.70 (316/451)
	2002	0.78 (286/366)	0.71 (320/450)
2001	2002	NA -----	0.65 (194/298)
	2003	NA -----	0.96 (136/142)

Discussion

Results of all transportation studies clearly indicate that transported fish have a differential survival (D) (they survive at lower rates) downstream of Bonneville Dam compared to fish that migrated through the hydropower system (they survive at higher rates). Even so, for yearling chinook salmon and steelhead, except for possibly at the very beginning of the season, transported fish return at the same or higher rates than fish migrating through the reservoirs and dams in the FCRPS. For subyearling migrants, it doesn't appear that transportation consistently provides higher returns of fish. In fact, in many comparisons, the fish that migrated through reservoirs and dams had higher return rates (due to very low sample sizes statistically higher returns were not detectable) than those transported. The higher returns occurred even though the presumed - but not directly measured - survival of the migrants is generally quite low.

Yearling chinook salmon transported by barge from Snake River dams arrive to their release point below Bonneville Dam typically in about 1.5 days while those that migrate through the 7 remaining dams take from 3 to 4 weeks early in the migration season, to less than 2 weeks by the end of May (Smith 2000b; Smith 2000a; Zabel 2001). Thus, smolts marked on the same day, but either transported or returned to the river most likely encountered different physical and biological conditions within the estuary and nearshore ocean upon their arrival. The Columbia River estuary and nearby ocean are very dynamic environments. Coastal winds, upwelling, currents, sea surface temperatures, and other physical conditions such as plume structure can change very quickly (Garcia Berdeal 2002). Large changes in biological conditions (such as forage fish abundance and predatory fish abundance) in the plume (Emmett 2000; Emmett 2001) and the estuary (R. L. Emmett, NOAA Fisheries, personal communication) have been observed between and within years. Growth and survival of salmonids in their first days and months at sea appear critical in determining overall salmonid year class strength. This is based on the relationship between returns of jack salmon with numbers of adults returning from the same brood class in later years, and between ocean purse seine catches of juvenile salmonids in June and subsequent jack and adult returns (Pearcy 1992).

Since transported fish generally enter the ocean 2 to 3 three weeks prior to in-river migrants, they most likely face greatly differing environmental conditions. Therefore, much of the observed seasonal average delayed mortality for transported fish could simply result from varying ocean conditions at their time of ocean entry. This comports with estimates of D observed in fish we marked at dams and results reported in the CSS where D was lowest for the earliest migrating stocks (Lookingglass and Dworshak hatcheries) and highest for the later migrants from McCall and Imnaha River acclimation ponds ((CSS) 2003).

Our analyses of seasonal trends in post-Bonneville survival suggests that within-season variation could have important implications for management decisions that a single seasonal estimate of D would mask. If the efficacy of transportation is largely determined by time of ocean entry, then delay of arrival below Bonneville Dam for early migrating stocks should increase their survival. Alternatively, for early migrating hatchery stocks, later hatchery release dates might lead toward a later arrival date at transport dams. Unfortunately, at this time, we have no means to predict conditions that will exist when smolts first arrive in the estuary or ocean.

The smoltification process in salmonids causes morphological, behavioral, and physiological changes that affect downstream migration as well as the ability to survive in the marine environment. This process is regulated by developmental stage, photoperiod, and water temperature cues that enable salmonids to migrate when environmental conditions are most favorable for downstream passage and survival in the seawater environment (Folmar 1980; Wedemeyer 1980). The act of migration further stimulates smolt development (Muir 1994; Zaugg 1985). Spring-summer chinook salmon and steelhead migrations in the Snake and Columbia Rivers show the same seasonal patterns each year, beginning in early April and tailing off near the end of May. Zaugg and Wagner (1973) found that gill Na^+-K^+ ATPase (an indicator of migratory readiness) and migratory urge declined at water temperatures of 13ºC and above. Steelhead that migrate too late in the season when water temperatures are above this threshold may have a tendency to residualize. Although this same behavior has not been demonstrated in spring-summer chinook salmon, exposure to water temperatures above 13ºC has been shown to retard gill Na^+-K^+ ATPase activity (Muir 1994). Furthermore, Congelton et al.(2004)found that hatchery spring-summer chinook salmon arriving at the collector dams had depleted the majority of their energy reserves, and for those fish left in river to migrate, deplete them further as they progressed downstream. Energy depletion was greater for smolts arriving at the dams later in the migration season and during the prolonged migration observed during the 2001 low flow year. Construction of the FCRPS has altered the timing of smolt migrations. Regardless of when fish arrive at Lower Granite Dam, those not transported most certainly take longer to migrate through the entire FCRPS and arrive later at the ocean and likely in different condition than they did historically. Further, transported fish cover the distance more quickly and arrive at the ocean sooner than they would have in an unregulated system.

The hypotheses that transportation induced stress or disease transmission (Budy et al. 2002) causes lower adult returns is not supported by the temporal variability in measured values of D and SARs. If these hypotheses held true, we would not expect to see the much higher SARs and D values later in the season. It appears more likely that early transported fish arrive too soon to the estuary.

Although D values below 1.0 indicate a differential mortality between transported and in-river migrants, we expect that some of the fish transported would die due to natural selection if they had continued their downstream migration through the hydropower system. Very low values of D, however, indicate a substantial differential mortality after release from transportation barges compared to the fish that survived to below Bonneville Dam after migrating through the reservoirs and dams of the FCRPS. Aside from a differential mortality between the upper dams on the Snake River from where they were transported (2% assumed), compared to fish that migrated to below Bonneville Dam (ca. 50% mortality), the two groups marked on the same day have substantially different timing to the ocean (a differential ranging from 20-25 days for the earliest fish to 15 days or less for the latest fish). This difference in timing likely accounts for D values greater than 1 often observed nearer the end of the migration period. We presume that the late migrants leaving Lower Granite Dam miss the “window of opportunity” for the best survival conditions by arriving too late below Bonneville Dam. The declining lipid reserves for late migrants observed by Congelton et al.(2004) might also play a role.

Nonetheless, on average, when the annual weighted D is matched with the average survival through the hydropower system, for wild spring summer chinook salmon, it provides an overall survival estimate for the entire stock of approximately 50%. This value is as high or higher than the estimated survival of juvenile fish migrating through the FCRPS when only 4 dams and reservoirs existed during the 1960s (Williams et al. 2001).

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With the low number of adult returns of PIT-tagged fish to date, especially for wild fish, definitive conclusions are not possible. We tentatively conclude that D-values for fish transported from McNary Dam are lower than for dams farther upstream. Combined with the higher survival to Bonneville Dam for fish left in the river at McNary Dam, a spring transportation program at McNary Dam will likely provide only marginal benefits (at best) to Snake River stocks. There is no evidence that D-values for chinook salmon transported from Little Goose Dam are lower than for fish transported from Lower Granite Dam.

Although annual SARs for fish PIT-tagged above Lower Granite Dam generally exceed those of fish PIT-tagged at Lower Granite, ratios of return rates of transported to not-detected fish (migrate past dams through turbines and spill) are similar. Thus, results from studies with fish PIT-tagged at Lower Granite Dam provided information on the relative differences in return rates of transported and in-river migrant fish in the population. The numbers of wild fish tagged above Lower Granite Dam estimated to have arrived at the dam were very small, and the vast majority of these fish were bypassed back to the river; therefore, the SARs of transported and non-detected wild fish tagged above Lower Granite Dam had large standard errors. This made statistical power very low to show differences in return rates among fish with different juvenile migration histories.

If D varies from location to location, a combination of strategies at different locations might maximize survival of in-river migrants. For instance, if D is high for fish transported from Lower Granite Dam, but low for fish transported from dams farther downstream, it might make sense to choose configurations and operations to maximize collection and transportation of smolts at Lower Granite Dam, but to not collect and transport fish at downstream dams. This strategy would involve eliminating or reducing spill at Lower Granite Dam and spilling to cap and full bypass operations at all other dams. Options to change collection strategies at dams to potentially benefit spring chinook salmon, of course, may have no effect or negative effect for other species.

For subyearling chinook salmon, transportation appears to neither greatly harm nor help the fish, and thus a combination of transportation and providing good conditions for fish not collected and transported is consistent with a “spread the risk” strategy until more is known.

JUVENILE MIGRANT SURVIVAL

Methods

Reach survival estimates

All mainstem dams on the lower Snake and Columbia Rivers, except The Dalles Dam, have juvenile fish bypass facilities (Fig. 1) (Matthews et al. 1977). These systems use screens to divert migrant smolts away from turbine intakes and into gatewells. Fish pass out of gatewells through orifices into a collection channel, where they pass directly to a pipe that discharges them to the tailrace, or they pass through a dewatering section leading to sampling or collection facilities. With the exception of Ice Harbor Dam, all bypassed fish pass through detectors that identify nearly 100% of PIT-tagged fish. PIT-tagged fish detected in the facilities at Lower Granite, Little Goose, Lower Monumental, and McNary dams ("collector", or "transport dams") are routed to raceways for loading into trucks or barges for transportation, or routed back to the river via a slide gate (Marsh 1999). The most downstream site for detections of PIT-tagged juvenile fish is in the Columbia River estuary between RKm 65 and 84, where a 2-boat trawl tows a PIT-tag detector (Ledgerwood 2000).

We estimate survival probabilities for juvenile migrant fish from PIT-tag detection histories. The estimated survival probability for a particular segment of the migration corridor is a group-level statistic, interpreted as an estimate of the proportion of the group that survived the segment. Collections of PIT-tagged fish are defined as a "group" for survival estimation in three primary ways: (1) fish tagged at the same time and released as a batch at a single point (typical for studies planned to address a specific research question, and for daily samples of fish collected at a smolt trap); (2) tagged fish held together in a holding facility for a period of time and then released from the same point over a short period of time (typical for volitional releases from hatcheries); (3) tagged fish released at various sites upstream from a particular dam, then grouped according to the date on which they were detected at the dam and returned to the tailrace (typical for attempts to gather a time series of survival estimates throughout the migration season). For estimates and analyses reported here, groups sometimes contain both hatchery and wild fish, or we treat the two rearing types separately. In all cases, a "group" of fish includes fish of only one species.

No matter how the group is defined, survival probabilities are estimated using the collection of records of detection ("detection histories") for every individual fish in the group. Because each PIT tag is uniquely coded, and because returning a portion of detected fish to the river allows detection at multiple dams, we analyzed the detection history data using a multiple-recapture model for single release groups. We use a model originally presented and investigated by Cormack (1964), Jolly (1965), and Seber (1965), known as the "CJS Model" or "Single-

Release (SR) Model." Use of this model for survival estimation using PIT-tagged fish was first described in detail by (Skalski 1998).

Minimum requirements for survival estimation using the SR are the release of a group of PIT-tagged fish at the beginning of the river segment of interest, one detection site where at least some of the detected fish are returned to the river for subsequent detection opportunities, and at least one detection site farther downstream. If there were only one detection site downstream from the release site, or if all detected fish at the first site were removed from the river, then it would be impossible to distinguish failure to detect a passing (surviving) fish from mortality before arrival at the detection site (i.e., survival probabilities could not be estimated separately from detection probabilities). Fish detected downstream from the first detection site constitute a sample of the fish that were alive at the first site; they are used to estimate the proportion of fish passing the first site that were detected (detection probability). Having obtained the estimate of the detection probability, we can then estimate the survival probability. When there is a series of detection sites with return-to-river capabilities, survival estimates are possible from release to the first site, then between each pair of consecutive sites, except that the inability to distinguish mortality from the failure to detect a surviving fish always precludes estimation between the last two sites.

In 1993, when a study specifically designed to estimate migrant smolt survival began, PIT-tag detectors were operational only at Lower Granite, Little Goose, Lower Monumental, and McNary Dams. Only Lower Granite and Little Goose Dams were equipped with slide gates to divert PIT-tagged fish from the bypass system back to the river. Under this configuration, we could only estimate survival for groups of fish from the point of release above Lower Granite Dam to the Lower Granite Dam tailrace and from Lower Granite Dam tailrace to Little Goose Dam tailrace. PIT-tag detectors and slide-gates were added gradually to other dams after 1993 (in a downstream direction). Under present conditions, provided sufficient fish from the group are detected by the estuarine trawl, we can estimate survival for any group of PIT-tagged fish from any release point upstream from Bonneville Dam to the tailrace of Bonneville Dam.

Here, we present all survival estimates from point of release (or the tailrace of a dam) to the tailrace of a dam downstream. All survival and detection probability estimates were computed using the statistical computer program SURPH ("Survival with Proportional Hazards") for analyzing release-recapture data, developed at the University of Washington (Skalski 1993; Smith 1994).

Assumptions of single-release model

Using the SR Model, the passage of a single PIT-tagged salmonid through the hydropower system is modeled as a sequence of events. Examples of such events are survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam, and detection at Little Goose Dam. Each event has an associated probability of occurrence. The detection history is the record of the outcomes of the events. (As previously noted, the detection history is an imperfect record of outcomes; if the history ends with one or more “zeroes,” we cannot distinguish mortality from survival without detection). The SR Model represents detection history data for a group of tagged fish as a multinomial distribution; each multinomial cell probability (detection history probability) is a function of the underlying survival and detection event probabilities. Estimates of survival probabilities under the SR Model are random variables, subject to sampling variability. When true survival probabilities are close to 1.0 and/or when sampling variability is high, it is possible for estimates of survival probabilities to exceed 1.0. For practical purposes, estimates should be considered equal to 1.0 in these cases.

Three key assumptions lead to the multinomial cell probabilities used in the SR Model:

A1) Fish in a single group of tagged fish have common event probabilities (each conditional detection or survival probability is common to all fish in the group).

A2) Event probabilities for each individual fish are independent from those for all other fish.

A3) Each event probability is conditionally independent from all other probabilities.

For a broader description of these assumptions and how they may be tested, see Burnham et al. (1987)and Zabel et al. (2002).

To varying degrees, these assumptions are inevitably violated for any particular group of migrating salmonids. Reasons that the assumptions might not strictly hold are: variation in fitness among fish in a group; variation in migration rate means, for example, that individuals from the same group may pass a dam under different conditions; inherent traits or behavioral preferences might make detection of some fish more likely at all dams.

Violations of model assumptions can cause bias in resulting parameter estimates. However, known causes and degrees of SR Model violations for migrating juvenile salmonids have been investigated, and have been shown to cause minimal bias (Skalski 1998). Studies are planned and analyses are designed to minimize the potential of significant bias due to violation of model assumptions.

Data sources and limitations

Information for juvenile salmonids PIT tagged and released in the Columbia River basin was obtained from the regional PTAGIS database (information available at www.psmfc.org). We grouped fish by migration year, species, run, rearing type, release site, and in some cases by date or time period.

Sometimes, due to small or zero sample sizes at the most downstream observation sites, caused by very poor survival to those sites and/or low detection rates at those sites, survival for some cohorts for the MCN-JDA and/or JDA-BON reaches was not estimated or alternate survival estimates were calculated by using the pooled estimate for a particular species-run-rearing type. In particular, estimates to Bonneville Dam were not calculated for mid-Columbia and Yakima groups until 2001 and 2002, respectively.

Our estimates were calculated only using information available from PTAGIS. We were certainly not aware of all the various experimental caveats and details involved in the studies for which many of the fish were tagged. Thus, although we used available PIT-tagged fish for survival estimates, we recognize that not all fish were released for the single purpose of estimating downstream reach survival. Therefore, some survival estimates, even if mathematically "correct," may not reflect or represent the true survival of the untagged population to which inference is intended.

Annual average survival estimates from Lower Granite and McNary dams

Between 1993 and 2003, hatchery and wild yearling chinook salmon and steelhead have been tagged in varying numbers at various locations upstream from Lower Granite Dam. Studies have also been conducted involving fish collected and tagged at Lower Granite Dam and then released into the tailrace. For survival estimation each year, we created daily "release groups" from Lower Granite Dam by combining fish tagged at the dam and released into the tailrace with previously tagged fish that were detected at the dam and returned to the tailrace the same day. For each daily group, detection data downstream from Lower Granite Dam was usually sufficient to calculate SR-Model survival estimates between Lower Granite and Little Goose dams, between Little Goose and Lower Monumental dams, and between Lower Monumental and McNary dams. If data for a daily group were not sufficient, we pooled adjacent days until estimates to McNary Dam were possible.

To obtain survival estimates downstream of McNary Dam, we regrouped fish into daily groups at McNary Dam, using the same methods described above for Lower Granite Dam. Detection data downstream from McNary Dam were usually not sufficient for each daily group. Therefore, we pooled the daily groups into weekly groups. For weekly groups leaving McNary Dam, we estimated survival between McNary and John Day Dams, and between John Day and Bonneville Dams.

Using these methods, we obtained estimates for particular river sections from multiple groups of PIT-tagged fish throughout each migration season. Annual average estimates for these river sections were obtained using a mean weighted by relative variability of the estimate; this method resulted in survival estimates with little or no bias (Muir et al. 2001).

Annual average survival estimates through the entire hydropower system

For Snake River yearling chinook salmon and steelhead, we estimated the annual mean survival probability from the head of Lower Granite Dam reservoir to Bonneville Dam tailrace. We calculated this estimate by multiplying three components: the estimate of survival from the Snake River Trap (near the head of the reservoir) to Lower Granite Dam (hatchery and wild fish pooled); the weighted mean survival estimate for daily groups from Lower Granite Dam tailrace to McNary Dam tailrace; and the weighted mean estimate for weekly groups from McNary Dam tailrace to Bonneville Dam tailrace.

Probability of detecting PIT-tagged fish versus length at tagging

Zabel et al. (in review) estimated the relationship between detection probability (at Little Goose, Lower Monumental and McNary Dams) versus length at tagging for spring-summer chinook salmon and steelhead (hatchery and wild) PIT tagged and released at Lower Granite Dam during the years 1998 through 2002. Here, we briefly present the methods and results of this analysis. More details are contained in Zabel et al. (in review).

Data

Study fish were yearling chinook salmon and steelhead of both wild and hatchery origin. The fish were captured, PIT-tagged, and released at Lower Granite Dam as part of transportation studies (Harmon et al. 2000; Marsh 2001). We analyzed control fish that were released to the tailrace. Our analysis comprised all release groups by species and origin from 1998-2002 that contained at least 10,000 fish released in a year. Because survival and detection probabilities may vary over a season, we divided each yearly release group into six weekly release groups over the period April 10 to May 21. The tagged fish were potentially detected in the bypass systems at Little Goose, Lower Monumental, McNary, John Day, and Bonneville Dams (Fig. 1). We combined detections at the last two sites together to increase the sample size, so an individual fish had four opportunities for detection.

Survival and detection probability estimation

First, we introduce three terms (based on terminology from (Lebreton et al. 1992)) for the site-specific survival and detection probabilities: ϕ_{nw} is the probability of fish released in week *w*

(w = 1,2,…,6) surviving through the nth river segment (n = 1,2,3); p_{nw} is the probability of detecting an individual from the wth release group at the nth detection site given the individual was alive at that site; and β_w is the combined probability for fish released in week w of surviving the last river segment and being detected at the last site, since the data cannot distinguish between these two probabilities. To incorporate length of fish into the analysis, we modified the CJS model (see (Zabel and Achord 2004)for details) by expressing survival and detection probabilities as functions of fish length. We used a logit link to ensure that survival and detection probabilities ranged from 0 to 1. For example, the relationship for fish released in week w between detection probability at site n and length was:

$$p_{nw}(l) = \frac{\exp(\alpha_{0,nw} + \alpha_{l,n} \cdot l)}{1 + \exp(\alpha_{0,nw} + \alpha_{l,n} \cdot l)}$$

where l is fish length (standardized to have zero mean) and the α's are coefficients. Note that we allowed overall survival and detection probabilities (i.e., the intercept terms) to vary by weekly release group, but we kept site-specific length effects constant across a season to keep the analysis tractable. If length was not included in the probability, the above equation reduced to $p_{nw} = \exp(\alpha_{0,nw})/1 + \exp(\alpha_{0,nw})$, which is a constant. When all survival and detection probabilities were related to length, we referred to the model as $\phi_1(l)\phi_2(l)\phi_3(l)p_1(l)p_2(l)p_3(l)$.

Model parameters were estimated using maximum likelihood (Mood et al. 1974). The likelihood function was numerically optimized with respect to the parameters. Standard errors were estimated based on numerical approximations of the Hessian matrix (Burnham et al. 1987). We used the readily-available software MARK (White and Burnham 1999)and SURPH (Lady et al. 2001)to conduct all analyses.

We constructed alternative models by either including or not including length relationships in each of survival and detection probabilities. To compare alternative models, we used likelihood ratio tests (LRT, (Mood et al. 1974)). The LRTs were designed such that they compared a null model to a more-complex alternative model. We implemented a "top-down" approach to the model selection process. In other words, we began with a full model, $\phi_1(l)\phi_2(l)\phi_3(l)p_1(l)p_2(l)p_3(l)$, where all survival and detection probabilities were related to length. Then we determined if we could remove individual length relationships (in either a survival or detection probability) based on a LRT. At each step, we chose the candidate length relationship for testing whose length coefficient (α_l) had the lowest coefficient of variation (CV, mean/standard error). If the null hypothesis of the LRT was not rejected (there was no support for inclusion of the length term in the model), then the length term was removed from the model.

Then, we designated this simpler model as the alternative model and attempted to remove an additional length term. We repeated the process until we rejected a null hypothesis and thus accepted the more complex alternative model.

Once we completed our model selection analyses, we focused on an additional question: how does the existence of length-related recapture probabilities affect our ability to estimate population-wide survival? In particular, does the commonly-used CJS model, which ignores variability in recapture probabilities among individuals, produce biased results? To address this question, we estimated population survival using two methods:

Method 1: Ignore length relations in detection and survival probabilities and use the CJS model, $\phi_1\phi_2\phi_3 p_1 p_2 p_3$. The weekly survival estimates were combined into a seasonal mean, with each weekly estimate weighted by the number of fish released per week.

Method 2: Include length-related detection probabilities where appropriate but ignore length effects on survival. In other words, use model $\phi_1\phi_2\phi_3 p_1(_*) p_2(_*) p_3(_*)$, where "$_*$" means include the length relationship or not depending on results from the model selection process. Again, weekly survival estimates were combined into a weighted mean for the season.

Results

Snake River yearling chinook salmon survival

Hatchery release groups

Seven hatcheries in the Snake River Basin released PIT-tagged yearling spring/summer chinook salmon each year between 1993 and 2003: Dworshak, Kooskia, Lookingglass, Rapid River, McCall, Pahsimeroi, and Sawtooth. For each hatchery each year we identified the group of PIT-tagged fish that was most representative of the hatchery's production release. For these groups of yearling chinook salmon we calculated estimates of survival from release to the tailrace of Lower Granite Dam. Many of these groups were released as a batch on a single occasion; others were released volitionally over a period of days from hatchery ponds or raceways.

Mean estimated survival from Snake River Basin hatcheries to the tailrace of Lower Granite Dam (average for hatcheries combined) has ranged from a low of 0.494 in 1997 to 0.697 in 2000. For all hatcheries, average survival has been higher since 1998 than it was in 1993 through 1997 (Table 16). A strong inverse relationship exists between survival and migration distance ($r^2 = 0.941$, $p<0.001$) (Fig. 20), with mean survival highest (0.765) from Dworshak National Fish Hatchery, 116 km from Lower Granite Dam, and lowest (0.403) from Sawtooth National Fish Hatchery, 747 km from Lower Granite Dam. However, survival from Sawtooth and Pahsimeroi hatcheries has improved in recent years, likely due to better control of bacterial kidney disease, weakening the relationship between distance and survival to Lower Granite Dam.

Table 16. Estimated survival for yearling chinook salmon from Snake River Basin hatcheries to the tailrace of Lower Granite Dam, 1993-2003. Distance from each hatchery to Lower Granite Dam in parentheses in header. Standard errors in parentheses following each survival estimate.

Year	Dworshak (116)	Kooskia (176)	Imnaha River weir (209)	Rapid River (283)	McCall (457)	Pahsimeroi (630)	Sawtooth (747)	Mean
1993	0.647 (0.028)	0.689 (0.047)	0.660 (0.025)	0.670 (0.017)	0.498 (0.017)	0.456 (0.032)	0.255 (0.023)	0.554 (0.060)
1994	0.778 (0.020)	0.752 (0.053)	0.685 (0.021)	0.526 (0.024)	0.554 (0.022)	0.324 (0.028)	0.209 (0.014)	0.547 (0.081)
1995	0.838 (0.034)	0.786 (0.024)	0.617 (0.015)	0.726 (0.017)	0.522 (0.011)	0.316 (0.033)	0.230 (0.015)	0.576 (0.088)
1996	0.776 (0.017)	0.744 (0.010)	0.567 (0.014)	0.588 (0.007)	0.531 (0.007)	—	0.121 (0.017)	0.555 (0.096)
1997	0.576 (0.017)	0.449 (0.034)	0.616 (0.017)	0.382 (0.008)	0.424 (0.008)	0.500 (0.008)	0.508 (0.037)	0.494 (0.031)
1998	0.836 (0.006)	0.652 (0.024)	0.682 (0.006)	0.660 (0.004)	0.585 (0.004)	0.428 (0.021)	0.601 (0.033)	0.635 (0.046)
1999	0.834 (0.011)	0.653 (0.031)	0.668 (0.009)	0.746 (0.006)	0.649 (0.008)	0.584 (0.035)	0.452 (0.019)	0.655 (0.045)
2000	0.841 (0.009)	0.734 (0.027)	0.688 (0.011)	0.748 (0.007)	0.689 (0.010)	0.631 (0.062)	0.546 (0.030)	0.697 (0.035)
2001	0.747 (0.002)	0.577 (0.019)	0.747 (0.003)	0.689 (0.002)	0.666 (0.002)	0.621 (0.016)	0.524 (0.023)	0.653 (0.032)
2002	0.819 (0.011)	0.787 (0.036)	0.667 (0.012)	0.755 (0.003)	0.592 (0.006)	0.678 (0.053)	0.387 (0.025)	0.669 (0.055)
2003	0.720 (0.008)	0.560 (0.043)	0.715 (0.012)	0.691 (0.007)	0.573 (0.006)	0.721 (0.230)	0.595 (0.149)	0.654 (0.028)
Mean	0.765 (0.026)	0.671 (0.032)	0.665 (0.015)	0.653 (0.034)	0.571 (0.024)	0.526 (0.045)	0.403 (0.052)	

Salmon and Snake River trap release groups

We also estimated survival from release to Lower Granite Dam for wild and hatchery PIT-tagged yearling chinook salmon and steelhead from the Salmon River (White Bird) and Snake River smolt traps. While fish are tagged and released nearly daily from these traps, daily groups rarely have sufficient data to calculate reliable survival estimates. For traps, then, we pooled all fish tagged and released between the beginning of operations in the spring and 31 May.

Estimated survival to the tailrace of Lower Granite Dam for yearling chinook salmon PIT-tagged at the Salmon River trap, 233 km upstream from Lower Granite Dam, averaged 0.777 for hatchery fish and 0.862 for wild fish between 1993 and 2003 (Table 17).

Table 17. Estimated survival for yearling chinook salmon from the Salmon River (Whitebird) trap to Lower Granite Dam tailrace (233 km), 1993-2003. Standard errors in parentheses. Simple arithmetic means across all years are given.

Year	Yearling Hatchery Chinook Salmon	Yearling Wild Chinook Salmon
1993	0.782 (0.019)	0.832 (0.014)
1994	0.761 (0.024)	0.817 (0.017)
1995	0.802 (0.012)	0.863 (0.011)
1996	0.735 (0.026)	0.822 (0.029)
1997	NA	NA
1998	0.740 (0.012)	0.926 (0.016)
1999	0.800 (0.013)	0.909 (0.012)
2000	0.806 (0.015)	0.920 (0.021)
2001	0.819 (0.007)	0.878 (0.009)
2002	0.792 (0.016)	0.844 (0.016)
2003	0.728 (0.016)	0.807 (0.011)
Mean	0.777 (0.010)	0.862 (0.014)

Estimated survival from the Snake River trap, at the head of Lower Granite Reservoir 52 km upstream from Lower Granite Dam, to the tailrace of Lower Granite Dam averaged 0.929 for hatchery yearling chinook salmon and 0.935 for wild yearling chinook salmon between 1993 and 2003 (Table 18).

Table 18. Estimated survival for yearling chinook salmon from the Snake River trap (near head of Lower Granite Reservoir) to Lower Granite Dam tailrace (52 km), 1995-2003. Standard errors in parentheses. Simple arithmetic means across all years are given.

Year	Yearling Hatchery Chinook Salmon	Yearling Wild Chinook Salmon
1993	0.823 (0.016)	0.847 (0.024)
1994	0.951 (0.029)	0.913 (0.036)
1995	0.886 (0.013)	0.944 (0.015)
1996	0.974 (0.032)	0.984 (0.039)
1997	NA	NA
1998	0.928 (0.013)	0.915 (0.019)
1999	0.930 (0.013)	0.950 (0.011)
2000	0.911 (0.018)	0.951 (0.023)
2001	0.956 (0.015)	0.921 (0.058)
2002	0.925 (0.027)	0.985 (0.038)
2003	1.001 (0.030)	0.943 (0.033)
Mean	0.929 (0.016)	0.935 (0.013)

Annual average survival estimates from Lower Granite and McNary dams

Except for the low-flow year 2001, mean estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace in 1998-2003 was consistent from year to year, ranging from a low of 0.729 for wild chinook salmon in 2003 to a high of 0.791 for both hatchery and wild fish in 1999 (Table 19). In 2001, mean estimated survival was only about 55%. Over the 6 years, average estimated survival was nearly identical for hatchery (0.731) and wild (0.729) chinook salmon.

Data were not sufficient to estimate survival from McNary Dam tailrace to Bonneville Dam tailrace for any Snake River yearling chinook salmon until 1999. From 1999-2003 data were sufficient to estimate survival for pooled hatchery and wild groups, but not for the rearing types separately. Annual average estimates ranged from 0.501 in 2001 to 0.763 in 2002, and averaged 0.667 for the 5 years 1999-2003 (Table 19).

Table 19. Estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace and from McNary Dam tailrace to Bonneville Dam tailrace for hatchery and wild yearling chinook salmon, 1998-2003. Standard errors in parentheses. Simple arithmetic means across all years are given.

	Lower Granite to McNary		McNary to Bonneville
Year	Hatchery	Wild	Hatchery + Wild Pooled
1998	0.773 (0.012)	0.771 (0.015)	NA
1999	0.791 (0.007)	0.791 (0.014)	0.704 (0.058)
2000	0.763 (0.026)	0.775 (0.014)	0.640 (0.122)
2001	0.556 (0.019)	0.541 (0.027)	0.501 (0.027)
2002	0.759 (0.008)	0.768 (0.026)	0.763 (0.079
2003	0.746 (0.019)	0.729 (0.020)	0.728 (0.030)
Mean	0.731 (0.036)	0.729 (0.039)	0.667 (0.046)

Annual average survival estimates through the entire hydropower system

For yearling chinook salmon (hatchery and wild combined), estimated survival through the entire hydropower system, from the Snake River trap at the head of Lower Granite Reservoir to the tailrace of Bonneville Dam, through eight mainstem dams and reservoirs has ranged from 0.267 in the low-flow year of 2001 to 0.551 in 2002 (Table 20).

Table 20. Hydropower system survival estimates derived by combining empirical survival estimates from various reaches for Snake River yearling chinook salmon (hatchery and wild combined), 1997-2003. Standard errors in parentheses. Abbreviations: Trap-Snake River Trap; LGR-Lower Granite Dam; BON-Bonneville Dam.

Year	Trap-LGR	LGR-BON	Trap-BON
1997	NA	NA	NA
1998	0.925 (0.009)	NA	NA
1999	0.940 (0.009)	0.557 (0.046)	0.524 (0.043)
2000	0.929 (0.014)	0.486 (0.093)	0.452 (0.087)
2001	0.954 (0.015)	0.279 (0.016)	0.266 (0.015)
2002	0.953 (0.022)	0.578 (0.060)	0.551 (0.057)
2003	0.993 (0.023)	0.532 (0.023)	0.528 (0.023)

Comparison of wild and hatchery yearling chinook salmon

Wild yearling chinook salmon had nearly equal to slightly higher survival than hatchery-reared fish between the Salmon and Snake River traps and the tailrace of Lower Granite Dam (Tables 17 and 18). Hatchery and wild yearling chinook salmon had similar average estimated survival from the tailrace of Lower Granite Dam to the tailrace of McNary Dam, through 4 dams and reservoirs (Table 19). Annually, estimated survival has been similar for hatchery and wild yearling chinook salmon, with neither stock having consistently higher survival.

The similarity in survival between PIT tagged hatchery and wild fish through this reach and from the Snake River trap to the tailrace of Lower Granite Dam, about 50% of the hydropower system, supports the use of hatchery fish as surrogates for wild fish in estimating juvenile downstream migrant survival for these stocks.

Upper Columbia River yearling migrant survival

Fewer years of PIT-tag data exist for fish stocks from the Upper Columbia River basin compared to those in the Snake River Basin. Nonetheless, the data indicate that juveniles migrating from the two basins under normal flow conditions have similar survival (Tables 21 and 22 compared to Table 20). This was not the case in the 2001 low-flow year. Fish from the Upper Columbia River had higher estimated survival to the McNary Dam tailrace (hatchery releases) and sometimes Bonneville Dam tailrace (dam releases) than did fish from the Snake River. A spill program existed at upper Columbia River dams in 2001, but not at Snake River dams, thus possibly explaining some of the difference in survival. For fish released at dams, a

Table 21. Survival estimates for upper Columbia River yearling chinook salmon. Standard errors in parentheses. Hatchery and wild fish released upstream of Rock Island Dam are designated "Above RIS", hatchery fish released downstream of Rock Island Dam are designated "Below RIS", and wild fish released above the confluence of the Columbia and Yakima Rivers are designated "Above Yakima". Summer chinook released from Wells Hatchery are a separate category. Abbreviations: REL-release site, RRE-Rocky Reach Dam, MCN-McNary Dam, JDA-John Day Dam, BON-Bonneville Dam, RIS-Rock Island Dam.

Year	Release Site	N	REL-RRE	RRE-MCN	REL-MCN	MCN-JDA	JDA-BON	REL-BON
Hatchery spring chinook salmon								
1999	Above RIS	14,894	0.782 (0.030)	0.727[a] (0.053)	0.570[b] (0.015)	0.890[b] (0.018)		
2000	Above RIS	14,877	0.705 (0.028)	0.692[a] (0.088)	0.543[b] (0.051)	0.892[b] (0.064)		
2001	Above RIS	15,014	0.756 (0.014)	0.565 (0.015)	0.461 (0.036)	0.812 (0.051)	0.788 (0.264)	0.312 (0.024)
2002	Above RIS	404,138	0.799 (0.074)	0.642 (0.032)	0.522 (0.017)	0.856 (0.012)	0.867 (0.079)	0.400 (0.015)
2003	Above RIS	355,321			0.559 (0.025)	0.892 (0.006)	0.796 (0.044)	0.416 (0.040)
Hatchery summer chinook salmon								
1999	Wells Hatchery	5,998			0.390[b] (0.050)	1.258[b] (0.520)	0.995 (0.319)	0.374 (0.110)
2000	Wells Hatchery	5,997			0.208[b] (0.020)	0.582 (0.081)	0.695 (0.036)	0.146 (0.017)
	Above RIS	45,981			0.962 (0.011)	0.738 (0.012)	0.695 (0.036)	0.568 (0.208)
2001	Wells Hatchery	6,000	0.443 (0.031)	0.483 (0.061)	0.214[b] (0.020)	0.407[b] (0.100)		
	Above RIS	90,118			0.723 (0.026)	0.863 (0.018)	0.787 (0.067)	0.506 (0.020)
	Below RIS	113,333			0.817 (0.031)	0.922 (0.009)	0.788 (0.050)	0.601 (0.060)
2002	Wells Hatchery	5,992	0.591 (0.034)	0.759 (0.063)	0.450[b] (0.030)	0.792[b] (0.160)	1.202 (0.217)	0.304 (0.286)
	Above RIS	90,125			0.771 (0.024)	0.866 (0.013)	1.202 (0.217)	0.876 (0.060)
2003	Wells Hatchery	5,996			0.449 (0.025)	1.158 (0.456)		
	Above RIS	103,907			0.787 (0.034)	0.856 (0.035)	0.846 (0.024)	0.582 (0.030)
	Below RIS	117,149			0.767 (0.024)	0.942 (0.022)	0.667 (0.126)	0.492 (0.090)
Wild spring chinook salmon								
2003	Above RIS	6,402			0.324 (0.021)	1.072 (0.033)	0.740 (0.053)	0.233 (0.066)

[a] Includes data from Bickford et al. 2001

[b] Includes data from Columbia Basin Research (www.cbr.washington.edu/pitSurv/)

Table 22. Survival estimates for PIT-tagged Yakima River yearling chinook salmon. Standard errors in parnetheses. Fish released upstream of Roza Dam are designated "Above Roza" and fish released downstream of Roza Dam are designated "Below Roza". Abbreviations: REL-release site, PRO-Prosser Dam, MCN-McNary Dam, JDA-John Day Dam, BON-Bonneville Dam.

Year	Release Site	N	REL-PRO	PRO-MCN	REL-MCN	MCN-JDA	JDA-BON	REL-BON
Hatchery spring chinook salmon								
1999	Above Roza	39,702	0.517 (0.025)	0.909	0.472 (0.023)	0.929 (0.024)		
2000	Above Roza	40,417	0.474 (0.016)	0.712 (0.027)	0.339 (0.019)	0.683 (0.041)		
	Below Roza	7,929			0.749 (0.025)	0.683 (0.041)		
2001	Above Roza	41,234	0.313 (0.037)	0.638 (0.006)	0.201 (0.021)	0.757 (0.040)		
	Below Roza	895			0.496 (0.022)	0.812 (0.105)		
2002	Above Roza	40,701	0.395 (0.021)	0.732 (0.009)	0.289 (0.016)	0.938 (0.036)	1.150 (0.146)	0.348 (0.047)
	Below Roza	1,261			0.520 (0.030)	0.938 (0.036)	0.356 (0.186)	0.214 (0.104)
2003	Above Roza	41,671	0.378 (0.029)	0.660 (0.035)	0.253 (0.030)	1.041 (0.071)	0.914 (0.139)	0.227 (0.043)
	Below Roza	4,308			0.510 (0.022)	0.877 (0.079)	0.914 (0.139)	0.288 (0.079)
Wild spring chinook salmon								
1999	Above Roza	312	0.581 (0.089)	0.923 (0.192)	0.538 (0.084)	0.866 (0.056)		
	Below Roza	3,040			0.774 (0.022)	0.866 (0.056)		
2000	Above Roza	6,209	0.678 (0.065)	0.600 (0.027)	0.414 (0.044)	0.814 (0.055)		
	Below Roza	5,727			0.819 (0.036)	0.795 (0.048)		
2001	Above Roza	2,179	0.312 (0.010)	0.759 (0.027)	0.237 (0.011)	0.631 (0.070)		
	Below Roza	1,606			0.688 (0.019)	0.658 (0.055)		
2002	Above Roza	8,717	0.397 (0.021)	0.658 (0.044)	0.254 (0.026)	0.870 (0.054)	0.921 (0.424)	0.187 (0.085)
	Below Roza	3,022			0.643 (0.010)	0.870 (0.054)	0.626 (0.247)	0.267 (0.006)
2003	Above Roza	7,803	0.377 (0.016)	0.728 (0.024)	0.274 (0.015)	0.883 (0.113)	0.782 (0.288)	0.198 (0.071)
	Below Roza	9,333			0.637 (0.008)	0.768 (0.045)	1.156 (0.054)	0.549 (0.016)

stock effect may also have played a part. Yearling summer-fall chinook salmon released at Upper Columbia River dams also had higher survival from McNary Dam to Bonneville Dam, whereas spring chinook salmon from the Yakima River did not. Yakima River spring chinook salmon had survival similar to Snake River spring chinook in the lower river.

Snake River Subyearling fall chinook salmon survival

Summer-migrating subyearling fall chinook salmon have a much more complex migration pattern than spring-migrating salmonids, thus, results from PIT-tag studies do not fall into neat, discrete parts. Most data on fall chinook salmon survival come from studies using fish released upstream from Lower Granite Dam. Since 1992, Connor et al. (2003a) have beach seined, PIT-tagged, and released fall wild chinook in their rearing areas. Since 1995, NOAA Fisheries has also PIT-tagged subyearling fall chinook at Lyons Ferry Hatchery, trucked them upstream above Lower Granite Dam, and released them at a time and size to match wild subyearling fall chinook salmon in their rearing areas (Smith 2003). As travel time to the Lower Granite Dam typically averages one month or more from time of release after tagging, survival estimates to Lower Granite Dam represent survival during both rearing and migration (Connor et al. 2003a; Connor et al. 2003b; Smith 2003). Subyearling fall chinook salmon rear and develop physiologically as they migrate, and their migration rate increases with migration distance and increased size. Unlike yearling smolts that generally all migrate quickly to Lower Granite Dam, some fall chinook salmon don't begin migrating for months. Thus, standard techniques for yearling smolts to measure travel times or survival don't work as well. From 1995 to 2000, we released nearly 200,000 PIT-tagged smolts above Lower Granite Dam. Subsequently we detected only about 62,000. Of these nearly 15% were not detected at a Snake River dam until after 1 September of the year, some not until the following spring. For the "active" migrants, those that passed the Snake River dams in June, July, and August in the year of release for the hatchery fish, the median pooled travel time for all years from release to detection at Lower Granite Dam averaged 43.5 days (Smith 2003). Within each migration year, median migration rate between each pair of dams was substantially greater between Lower Monumental and McNary Dams and between McNary and Bonneville Dams than between pairs of dams upstream from Lower Monumental Dam (Fig. 21)

The survival of both wild and hatchery fish to Lower Granite Dam has varied widely among years and within years with survival declining as the migration season progresses, flows decrease, and water clarity and temperature increases (Connor et al. 2003a; Smith 2003). Certainly, a need exists for an estimated average survival through the Lower Granite Dam reservoir, but with data collected to date, we cannot partition what portion of the mortality occurred within the hydropower system, as measures of survival (and travel time) represent both rearing and migration.

Connor et al.(2003a) divided wild subyearling fall chinook salmon into four equally sized cohorts each year (1998-2000), and estimated 57-88% survival to Lower Granite Dam tailrace for the earliest migrating cohort PIT-tagged in early to mid-May to 36% for fish tagged in mid-June. For hatchery subyearling chinook salmon, estimated survival was 35-55% for early June releases, 16-49% for mid-June releases, and 2-24% for the last releases in early July for fish released near Asotin, Washington, at Billy Creek during those years (Fig.22) (Smith 2002; Smith 2003).

Estimating survival for subyearling chinook salmon below Lower Granite Dam has also been difficult. Because of lower detection efficiencies (because of lower fish guidance efficiencies for fall chinook), fewer PIT-tagged fish, poor survival to Lower Granite Dam, and fish dispersed over a wide time period, survival for Snake River fall chinook has only been estimated as far as the tailrace of Lower Monumental Dam, and only for fish of hatchery origin (Smith 2002; Smith 2003). Survival between the tailrace of Lower Granite Dam and the tailrace of Lower Monumental Dam has been highly variable, with a general decline in mid to late-August, and much lower overall than for spring migrating yearling chinook salmon (Fig. 23). We did not make a survival estimate over this reach in 2002. In 2003, estiamted survival between the tailraces of Lower Granite and McNary Dams ranged from 75% for fish leaving Lower Granite Dam the second week in June to 22% for fish leaving the second week in July.

We have no survival estimates for juvenile fish that migrated in September and October, nor for undetected fish. Based on adult returns, however, the two groups accounted for 14 and 36% of the total adult return of the in-river PIT-tagged fish (nearly all adult returns to Lower Granite Dam came from untagged fish transported from collector dams as juveniles).

Upper Columbia River subyearling migrant survival

Fewer years of PIT-tag data exist for fish stocks from the Upper Columbia River basin compared to those in the Snake River Basin. Depending on year and release site, survival values ranged widely (Tables 23 and 24).

Table 23. Survival estimates for PIT-tagged upper Columbia River subyearling chinook salmon (standard errors in parentheses) and percentage recovery of PIT-tagged fish on bird islands. Hatchery and wild fish released downstream of Rock Island Dam are designated "Below RIS", and wild fish released above the confluence of the Columbia and Yakima Rivers are designated "Above Yakima". Abbreviations: MCN-McNary Dam, JDA-John Day Dam, BON-Bonneville Dam, RIS-Rock Island Dam.

Year	Release Site	N	PIT-tag recovery on bird islands	REL-MCN	MCN-JDA	JDA-BON	REL-BON
Hatchery fall chinook							
1999	Below RIS	6,778	0.0081	0.800[a] (0.037)	0.720[a] (0.017)		
2000	Below RIS	6,091	0.0144	0.624[a] (0.068)	0.483[a] (0.069)		
2001	Below RIS	35,762	0.0063	0.667[a] (0.050)	0.683[a] (0.062)		
2002	Below RIS	66,554	0.0051	0.716[a] (0.019)	0.778[a] (0.030)	0.788 (0.116)	0.390 (0.040)
2003	Below RIS	81,253	0.0028	0.558 (0.034)	0.820 (0.042)		
Wild fall chinook							
1999	Above Yakima	5,042	0.0113	0.398 (0.024)	0.833 (0.119)		
2000	Above Yakima	10,967	0.0098	0.432 (0.035)			
2001	Above Yakima	9,481	0.0127	0.366 (0.025)	0.563 (0.029)		
2002	Above Yakima	414	0.0048	0.402 (0.058)	0.696 (0.290)		
2003	Above Yakima	2,975	0.0084	0.315 (0.020)	0.600 (0.122)		

[a] Includes data from Columbia Basin Research (www.cbr.washington.edu/pitSurv/)

Table 24. Survival estimates for PIT tagged Yakima River fall chinook salmon (standard errors in parentheses) and percentage recovery of PIT-tagged fish on bird islands. Fish released downstream of Roza Dam are designated "Below Roza". Abbreviations: REL-release site, PRO-Prosser Dam, MCN-McNary Dam, JDA-John Day Dam, BON-Bonneville Dam.

Year	Release Site	N	PIT-tag recovery on bird islands	REL-MCN		MCN-JDA		JDA-BON		REL-BON	
Hatchery fall chinook											
1999	Below Roza	7,324	0.0104	0.588	(0.108)	0.669	(0.053)				
2000	Below Roza	4,051	0.0222	0.645	(0.119)	0.573	(0.137)				
2001	Below Roza	3,979	0.0206	0.330	(0.037)	0.696	(0.113)				
2002	Below Roza	4,001	0.0165	0.223	(0.011)	0.867	(0.132)	0.723	(0.239)	0.149	(0.047)
2003	Below Roza	3,987	0.0025	0.183	(0.083)	0.783	(0.071)	0.716	(0.000)	0.147	(0.055)
Wild fall chinook											
1999	Below Roza	876	0.0011	0.790	(0.021)	0.720	(0.188)				
2000	Below Roza	1,979	0.0344	0.272	(0.025)						

Snake River steelhead survival

Hatchery release groups

Two hatcheries in the Snake River Basin released PIT-tagged fish most years between 1993 and 2003: Dworshak and Clearwater. Although we estimated survival for release groups, as the hatcheries released fish at a number of sites within the Clearwater basin, we did not tabulate survival the hatcheries to Lower Granite, as we did for yearling chinook salmon.

Salmon and Snake River trap release groups

Estimated survival to the tailrace of Lower Granite Dam for steelhead PIT-tagged at the Salmon River trap, 223 km above Lower Granite Dam, averaged 0.854 for hatchery fish and 0.869 for wild fish from 1993 - 2003 (Table 26).

Table 26. Estimated survival for steelhead from the Salmon River (Whitebird) trap to Lower Granite Dam tailrace (233 km), 1993-2003. Standard errors in parentheses. Simple arithmetic means across all years are given.

Year	Hatchery steelhead	Wild steelhead
1993	0.875 (0.011)	0.832 (0.019)
1994	NA	NA
1995	0.882 (0.013)	0.892 (0.025)
1996	0.851 (0.022)	0.956 (0.060)
1997	0.872 (0.017)	0.876 (0.062)
1998	0.879 (0.016)	0.892 (0.070)
1999	0.825 (0.014)	0.816 (0.039)
2000	0.870 (0.019)	0.815 (0.041)
2001	0.786 (0.009)	0.878 (0.019)
2002	0.814 (0.041)	0.780 (0.050)
2003	0.885 (0.028)	0.952 (0.092)
Mean	0.854 (0.011)	0.869 (0.018)

Estimated survival from the Snake River trap, at the head of Lower Granite Reservoir 52 km above Lower Granite Dam, to the tailrace of Lower Granite Dam averaged 0.927 for hatchery steelhead and 0.935 for wild steelhead from 1993 - 2003 (Table 27).

Table 27. Estimated survival for steelhead from the Snake River trap (near head of Lower Granite Reservoir) to Lower Granite Dam tailrace (52 km), 1995-2003. Standard errors in parentheses. Simple arithmetic means across all years are given.

Year	Hatchery steelhead	Wild steelhead
1993	0.917 (0.008)	0.898 (0.009)
1994	NA	NA
1995	0.936 (0.011)	0.955 (0.013)
1996	0.941 (0.020)	0.973 (0.022)
1997	0.963 (0.016)	0.968 (0.051)
1998	0.926 (0.010)	0.919 (0.017)
1999	0.908 (0.012)	0.910 (0.024)
2000	0.947 (0.014)	0.977 (0.027)
2001	0.893 (0.008)	0.958 (0.010)
2002	0.893 (0.019)	0.899 (0.023)
2003	0.946 (0.018)	0.893 (0.026)
Mean	0.927 (0.008)	0.935 (0.011)

Annual average survival estimates from Lower Granite and McNary dams

Except for the low-flow year 2001, mean estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace in 1998-2003 ranged from a low of 0.533 for hatchery steelhead in 2002 to a high of 0.746 for wild fish in 1999 (Table 28). In 2001, mean estimated survival was very low: 0.170 for hatchery steelhead and 0.168 for wild. Over the 6 years, average estimated survival was 0.533 for hatchery and 0.586 for wild steelhead.

Data were not sufficient to estimate survival from McNary Dam tailrace to Bonneville Dam tailrace for any Snake River steelhead until 1998. From 1998-2003 data were sufficient to estimate survival for pooled hatchery and wild groups, but not for the rearing types separately. Annual average estimates ranged from 0.250 in 2001 to 0.770 in 1998, and averaged 0.540 for the 6 years 1998-2003 (Table 28). Estimated survival between McNary Dam tailrace and Bonneville Dam tailrace was lower in all 3 years 2001-2003 than in any year 1998-2000.

Table28. Estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace and from McNary Dam tailrace to Bonneville Dam tailrace for hatchery and wild steelhead, 1998-2003. Standard errors in parentheses. Simple arithmetic means across all years are given.

	Lower Granite to McNary		McNary to Bonneville
Year	Hatchery	Wild	Hatchery + Wild Pooled
1998	0.644 (0.015)	0.698 (0.030)	0.770 (0.081)
1999	0.673 (0.019)	0.746 (0.019)	0.640 (0.024)
2000	0.574 (0.038)	0.714 (0.028)	0.580 (0.047)
2001	0.170 (0.013)	0.168 (0.010)	0.250 (0.016)
2002	0.533 (0.045)	0.593 (0.039)	0.488 (0.090)
2003	0.606 (0.028)	0.597 (0.022)	0.510 (0.015)
Mean	0.533 (0.075)	0.586 (0.087)	0.540 (0.071)

Annual average survival estimates through the entire hydropower system

For steelhead (hatchery and wild combined), estimated survival through the entire hydropower system, from the Snake River trap at the head of Lower Granite Reservoir to the tailrace of Bonneville Dam, through eight mainstem dams and reservoirs has ranged from a low of 0.038 in the low-flow conditions of 2001 to 0.462 in 1998 (Table 29).

Table 29. Hydropower system survival estimates derived by combining empirical survival estimates from various reaches for Snake River steelhead (hatchery and wild combined), 1997-2003. Standard errors in parentheses. Abbreviations: Trap-Snake River Trap; LGR-Lower Granite Dam; BON-Bonneville Dam.

Year	Trap-LGR	LGR-BON	Trap-BON
1997	0.964 (0.015)	0.474 (0.069)	0.457 (0.067)
1998	0.924 (0.009)	0.500 (0.054)	0.462 (0.050)
1999	0.908 (0.011)	0.440 (0.018)	0.400 (0.016)
2000	0.964 (0.013)	0.393 (0.034)	0.379 (0.032)
2001	0.911 (0.007)	0.042 (0.003)	0.038 (0.003)
2002	0.895 (0.015)	0.262 (0.050)	0.234 (0.045)
2003	0.932 (0.015)	0.309 (0.011)	0.288 (0.011)

Comparison of wild and hatchery steelhead

Wild steelhead had slightly higher survival than hatchery-reared fish between the tailrace of Lower Granite Dam and the tailrace of McNary Dam, through 4 dams and reservoirs (Table 28). For steelhead, estimated survival through this reach has averaged about 5% higher for wild fish (0.586) compared to steelhead of hatchery origin (0.533), with wild steelhead survival higher in 4 of the 6 years (Table 28).

Upper Columbia River steelhead survival

Fewer years of PIT-tag data exist for fish stocks from the Upper Columbia River basin than for those in the Snake River Basin. Nonetheless, the data indicate that juveniles migrating from the two basins under normal flow conditions have similar survival (Table 30 compared to Table 29). This was not the case in the 2001 low-flow year. Fish from the Upper Columbia River had higher estimated survival to the McNary Dam tailrace (hatchery releases) and sometimes Bonneville Dam tailrace (dam releases) than did fish from the Snake River. A spill program existed at upper Columbia River dams in 2001, but not at Snake River dams, possibly explaining some of the difference in survival. For fish released at dams, a stock effect may also have played a part.

Table 30. Survival estimates for upper Columbia and Yakima River steelhead. In the upper Columbia River, hatchery fish released upstream of Rock Island Dam are designated "Above RIS" and wild fish were released at Rock Island Dam. In the Yakima River, fish released downstream of Roza Dam are designated "Lower Yakima". Abbreviations: REL-release site, MCN-McNary Dam, JDA-John Day Dam, BON-Bonneville Dam, RIS-Rock Island Dam.

Year	Release Site	N	REL-MCN		MCN-JDA		MCN-BON	
Hatchery summer steelhead								
1999	Above RIS	134,251	0.616	(0.013)	1.016	(0.013)		
2000	Above RIS	63,227	0.607	(0.009)	0.861[a]	(0.059)		
2001	Above RIS	4,029	0.203	(0.029)	0.535	(0.146)	0.178	(0.078)
2002	Above RIS	3,623	0.529	(0.107)	1.119	(0.168)	0.856	(0.349)
2003	Above RIS	391203	0.447	(0.014)	1.027	(0.025)	0.800	(0.042)
Wild summer steelhead								
1999	Rock Island Dam	1,156	0.635	(0.055)	1.103	(0.148)		
2000	Rock Island Dam	1,200	0.679	(0.102)	0.873	(0.224)		
2001	Rock Island Dam	1,174	0.211	(0.022)	0.304	(0.082)		
2002	Rock Island Dam	1,200	0.623	(0.063)	0.680	(0.125)		
Wild spring-summer steelhead (Yakima)								
1999	Lower Yakima	1,241	0.798	(0.033)	0.967	(0.099)		
2002	Lower Yakima	1,335	0.314	(0.054)	0.924	(0.302)	0.560	(0.585)
2003	Lower Yakima	575	0.394	(0.099)	0.860	(0.359)		

[a] Includes data from Bickford et al., 2001

Snake River Sockeye salmon survival

We have little information about these fish. We see few juveniles at dams and nearly no adults have returned for the last decade, the latter in spite of efforts to raise fish in conservation hatcheries to increase numbers of juveniles in the outmigration. We did observe in 2003 that survival of juveniles from release to Lower Granite Dam was quite low (Table 31).

Table 31. Survival estimates for juvenile sockeye salmon released upstream from Lower Granite Dam, 2003. Standard errors in parentheses. Abbreviations: LGR-Lower Granite Dam; MCN-McNary Dam.

Hatchery	Release site	Number released	Survival to LGR	Survival to MCN
Sawtooth	Pettit Lake	2,013	0.444 (0.021)	0.308 (0.044)
Sawtooth	Redfish Lake	1,015	0.116 (0.016)	0.068 (0.023)
Bonneville	Alturus Lake	1,481	0.034 (0.017)	0.008 (0.003)
Bonneville	Pettit Lake	1,565	0.345 (0.024)	0.191 (0.047)
Bonneville	Redfish Lake	1,007	0.068 (0.015)	0.023 (0.008)

We can say that none of the efforts to improve survival of Snake River chinook salmon and steelhead have appeared to provide any benefits for Snake River sockeye salmon.

Probability of detecting PIT-tagged fish versus length at tagging

We analyzed data from over 340,000 PIT-tagged individuals in nine release groups. Detection probability was clearly related to fish length for all release groups: the model selection process chose length relationships in 21 out of 24 year/site combinations (Figs. 24 and 25). In 20 out of 21 cases where a length relationship was selected, the length coefficient, α_l, was negative, indicating that smaller fish had a higher probability of detection.

When we compared among the two methods for estimating population survival, we found a high level of correlation and little evidence for bias (Fig. 26). Comparing Method 1 to Method 2, the survival estimates produced by the two methods were very highly correlated (r = 0.999), and Method 1 produced survival estimates that averaged 0.02 percent less than those produced by Method 2.

Discussion

Avian predation

All PIT-tagged fish from the Snake River that survived to the McNary pool were subject to predation by piscivorus birds residing on various islands, including Caspian terns, double-crested cormorants, gulls, and pelicans. The bird colony locations included, but were not limited to, Richland Island, Island 18, Foundation Island, Badger Island, and Crescent Island. All of these islands are located in the McNary Dam reservoir - mostly above the confluence with the Snake River. Predation also occurred from birds residing in various locations below MCN to the mouth of the Columbia River and much of this information is contained in another Tech Memo on the role of the estuary in the recovery of Columbia River basin salmon and steelhead.

Since 1998, NOAA Fisheries researchers have visited bird colonies after the end of the nesting season and scanned for PIT tags. The recovery data are available from the PTAGIS database. To investigate the impact of avian predation from bird colonies in the McNary Dam pool, the most valuable information possible would be an estimate of the proportion of fish entering the pool that were taken by piscivorous birds. However, we have no PIT-tag estimates of survival to the head of McNary Dam pool. Instead, for Snake River fish we calculated the proportion of PIT-tagged fish that were detected as they passed Lower Monumental Dam whose tags were later detected on a bird colony. For fish from the Upper Columbia River, we calculated the proportion recovered on bird colonies of entire hatchery releases. Furthermore, we obtained records from PIT-tagged smolts only if the tag was deposited on a colony and in such a way that it was detectable. Thus, these proportions constitute minimum estimates of mortality from bird predation. When compared across cohorts of fish or across years, the proportions represent an index of relative impacts.

Between 1998 and 2003, the greatest avaian predation apparently occurred in the low-flow year 2001 (Table 32), a year in which over 10% of PIT-tagged steelhead released in the Upper Columbia River and more than 20% of PIT-tagged steelhead detected at Lower Monumental Dam were later recovered on bird colonies. However, PIT-tagged fish made up a much larger portion of all Snake River fish that remained in the river below Lower Monumental Dam; without spill a higher percentage of non-tagged fish were transported. Thus, the total number of salmonid smolts taken by avian predators in 2001 was probably not as elevated as suggested by these proportions. Nonetheless, as the survival estimates presented in the Results section are based on these PIT-tagged fish, increased avian predation on PIT-tagged fish is a partial explanation of the low estimates we obtained in 2001.

Table 32. Recovery percentages of PIT-tagged steelhead recovered from McNary pool bird colonies. Percentages based on number of fish detected at Lower Monumental Dam for Snake River fish and numbers released for Upper Columbia River fish.

Year	Snake River Yearling Chinook Salmon	Snake River Steelhead	Upper Columbia River Steelhead
1998	0.49	4.20	NA
1999	0.84	4.51	1.92
2000	0.98	3.66	2.36
2001	5.59	21.06	11.49
2002	1.19	10.09	3.81
2003[a]	1.06	3.71	1.34

[a] Only Crescent Island Caspian tern colony sampled

Snake River steelhead were taken by birds in much larger proportions than Snake River yearling chinook salmon. Recovery proportions for Upper Columbia River stocks were lower than for Snake River stocks, but this is partly because the release group numbers do not take into account mortality from release to the head of the McNary Dam reservoir (wide range in values of survival from release to McNary Dam). If mortality averaged 50% to that point, doubling these recovery proportions, then avian predators had similar affects on Upper Columbia River fish.

Probability of detecting PIT-tagged fish versus length at tagging

This analysis clearly demonstrated a negative relationship between detection probability and fish length for juvenile Snake River spring/summer chinook salmon and Snake River steelhead. Thus, bypassed fish do not represent a random sample of the migrant population. Fortunately, this relationship does not appear to bias CJS survival estimates. However, the results do call into question the conclusion of Budy et al. (2002) that passage through bypass systems results in delayed mortality. We discuss this in greater detail in the *Latent Mortality* section. Also, the results have implications for transportation studies. Transported and in-river control fish (non-detected fish) may represent different segments of the population, and this might partially explain the relatively poor performance of transported fish. This topic merits more detailed analyses in the future.

Travel time and survival

The following major section will provide more detail on travel time and survival, however, we note here that travel time appears to influence estimates of juvenile steelhead survival more than yearling chinook salmon. Although median annual travel times varied yearly for both chinook salmon and steelhead (see details below), a relatively similar annual survival estimate was derived for chinook salmon across years (Table 20). In contrast, for steelhead when median annual travel times increased beyond about 15 days, estimated annual survival decreased considerably (Table 29.)

JUVENILE SURVIVAL, TRAVEL TIME, AND RIVER ENVIRONMENT

Methods

Snake River spring migrants

Smith et al. (2002) investigated relationships among survival, travel time, and river conditions for migrant yearling chinook salmon and steelhead in the Lower Snake River. Their study included juveniles migrating through the river segment between Lower Granite and McNary Dam tailrace in the 1995 through 1999 migration seasons. The following is not intended as a comprehensive update of the findings of Smith et al. (2002). Instead, we address selected issues concerning relations of survival and travel time with river conditions that have arisen since the 1999 migration season. In particular, incorporation of observations from the low-flow year 2001 sheds light on responses of salmonids to conditions not previously observed since PIT-tag data became available. In what follows, we note when additional years of data did not alter previous conclusions, and describe instances where new information suggests new hypotheses to explain patterns.

As described in earlier sections, we used fish PIT tagged above and at Lower Granite Dam for migration years 1999 to 2003. We developed survival estimates as described in the previous section.

Median travel time

Travel times were calculated for yearling chinook salmon and steelhead for the reaches: 1) Lower Granite Dam to Little Goose Dam (60 km); 2) Little Goose Dam to Lower Monumental Dam (46 km); 3) Lower Monumental Dam to McNary Dam (199 km); 4) Lower Granite Dam to McNary Dam (225 km); 5) Lower Granite Dam to Bonneville Dam (461 km); 6) McNary Dam to John Day Dam (123 km); 7) John Day Dam to Bonneville Dam (113 km); and 8) McNary Dam to Bonneville Dam (236 km). Travel time between any two dams was calculated for each fish detected at both dams as the number of days between last detection at the upstream dam (generally at a PIT-tag detector close enough to the outfall site that fish arrived in the tailrace within minutes after detection) and first detection at the downstream dam. Travel time included the time required to move through the reservoir to the forebay of the downstream dam and any delay associated with residence in the forebay, gatewells, or collection channel prior to detection in the juvenile bypass system.

Migration rate through a river section was calculated as the length of the section (km) divided by the travel time (days) (which included any delay at dams as noted above).

For each group, the 20th percentile, median, and 80th percentile travel times and migration rates were determined. The true complete set of travel times for a release group includes travel times of both detected and not-detected fish. However, using PIT tags, travel times cannot be determined for a fish that traverses a river section but is not detected at both ends of the section. Travel time statistics are computed only from travel times for detected fish, which represent a sample of the complete set. Non-detected fish pass dams via turbines and spill; thus, their time to pass a dam is typically minutes to hours shorter than detected fish passing to the tailrace via the juvenile bypass system.

River environment variables

We used the methods of Smith et al. (2002) to calculate indices of exposure to various river condition variables, including river discharge ("flow") (kcfs), percentage of flow that passed over spillways, and water temperature (°C). Indices were calculated at Little Goose, Lower Monumental, and McNary Dam for each release group, based on the group's distribution of detections at each dam.

It has been suggested (e.g., FPC 2003), that exposure to water velocity is likely more important to the response of an individual migrant than exposure to flow volume. Accordingly, in addition to the indices used in Smith et al. (2002), the analyses in this section include a variable to reflect "water travel time" (WTT). We derived our "approximate" WTT variable from the flow exposure indices at Lower Monumental and McNary Dams and from figures 1 and 2 of the Fish Passage Center Annual Report 2002 (FPC 2003). For each daily release group from Lower Granite Dam, we calculated water travel time days from Lower Granite Dam to Ice Harbor Dam using the exponential decay equation (FPC 2003 Fig. 1):

$$28.97e^{-0.02148 f_1} + 3.160$$

where f_1 is the flow exposure index (kcfs) at Lower Monumental Dam, and from Ice Harbor Dam to McNary Dam using the equation (FPC 2003 Fig. 2):

$$12.12e^{-0.008776 f_2} + 1.232$$

where f_2 is the flow exposure index (kcfs) at McNary Dam. The total WTT for each group was the sum of these two components.

Mortality per day vs. water travel time

To investigate interactions among the relations of travel time, survival, and water travel time, we calculated the following quantity for each release group from Lower Granite Dam:

$$Mort.\,perDay = 1 - \hat{S}^{(1/TT)}$$

and examined its relationship to water travel time ($\hat{S}$ and TT are the group's estimated survival probability and median travel time from Lower Granite Dam to McNary Dam, respectively). For example, if fish travel time were positively related to water travel time, but reach survival were not, then the mortality per day must decrease as water travel time and fish travel time increase. Conversely, if mortality per day is constant, then a positive relationship between water travel time and fish travel time would induce a positive relationship between reach survival and water travel time.

Generalized additive models

We explored multiple regression (analysis of covariance) models that included year-effects variables and two or more quantitative environmental variables. Because the independent variables were correlated with each other, and because some relations had notable nonlinearity, we checked multiple regression models using the generalized additive model ("gam") function of S-Plus (MathSoft, Inc. 2000), a nonparametric multiple regression technique. The nonparametric splines calculated in the gam function were used to suggest parametric curve functions (polynomials) to use in parametric multiple regression models. Resulting multiple regression models were rejected if graphic inspection of residuals revealed remaining nonlinearity or notable lack of normality. Partial fits of predictor variables from the generalized additive models were plotted without vertical axis labels. The vertical axis in partial fit plots is transformed and scaled, making interpretation of units difficult. Relative influence of individual predictor variables can be gauged by the relative range of the partial fit functions, and the shape of the nonlinear relation between predictor and dependent variable can be seen.

Threshold models for survival vs. flow

As observed by Smith et al. (Smith et al. 2002), survival estimates varied little within seasons when the flow level was moderate to high. After accounting for differences in annual means, Smith et al. (Smith et al. 2002) found no relation between survival estimates for 1995-1999 and flow exposure for yearling chinook salmon, and only a weak relation for steelhead.

With additional years of data, the lowest survival estimates were observed in the lowest flow year, 2001. Along with the recognition that zero survival would likely result if there were zero flow and with the observation of little or no relation between flow and survival at moderate to high flow levels, the 2001 data suggests that there may be a "threshold effect" in the relation. That is, there may be a flow level above which survival has little variability, but below which there is a positive relationship with flow.

We have no hypothesized mechanism to suggest a theoretical basis for the exact "shape" of such a threshold relation (though we recognize that water travel time could be related to such a mechanism). However, we have explored two mathematical forms that might describe the relationship: a sigmoid curve and a broken-stick regression line.

The sigmoid curve had the following equation form ("Boltzmann sigmoid"):

$$Y = Bottom + \frac{(Top - Bottom)}{1 + e^{(V50 - X)/Slope}}$$

where *X* and *Y* were the independent (flow exposure index) and dependent (estimated survival) variable, respectively, and *Top*, *Bottom*, *V50*, and *Slope* were parameters to be estimated. A sigmoid curve is "S-shaped:" assuming positive *Slope*, the curve rises from low to high values of *X* and *Y*, with relative shallow slope at low and high ends of the range of *X* values, and steeper slope in the intermediate range. The *Bottom* and *Top* parameters are the minimum and maximum *Y*-values on the curve, respectively. The *V50* parameter is the *X* value for which *Y* is halfway between *Bottom* and *Top*, and *Slope* describes the steepness of the curve, with larger values denoting a shallower curve. We used this form only for estimated survival. In these models, the *Bottom* parameter was always set equal to 0.0.

The selected broken-stick regression model was the one that minimized sum of squared error among models that had the following properties: linear relationship between flow exposure and estimated survival when the exposure was below the threshold. No relationship when the exposure was above the threshold (survival constant, equal to the fitted value of the linear regression line at the threshold flow value). Selection of the threshold, or break point, was part of the least-squares optimization.

Both the sigmoid curve and the broken stick were fitted using unweighted least squares. For the broken-stick fit, we used bootstrap methods to characterize uncertainty in estimation of maximum survival, slope below the threshold, and most importantly, the threshold.

Results

Snake River yearling chinook salmon

Travel time vs. flow and water travel time

With the exception of the low flow year of 2001, the annual median travel time (days) for all PIT-tagged Snake River spring-summer chinook salmon passing between Lower Granite and Bonneville Dams from 1 April to 31 May each year varied by only a few days (Table 30.)

Table 30. Median travel time (days) of PIT-tagged yearling chinook salmon between Lower Granite Dam (LGR) and Bonneville Dam (BON), 1995-2003.

Year	Median LGR-BON travel time (days)
1995	18.4
1996	16.2
1997	14.1
1998	19.0
1999	16.1
2000	16.4
2001	31.0
2002	16.9
2003	14.4

Based on earlier data derived from Raymond (1979), these times were approximately 40-50% longer than when only 4 dams existed in the mainstem Snake and Columbia Rivers (Fig. 27).

Within individual years, median travel time for groups of PIT-tagged yearling chinook salmon has generally decreased throughout the migration season, as flows have generally increased (Fig. 28) (and water travel time has decreased - Fig. 29). However, water velocity is clearly not the only driver of travel time in all years: in 1998, and especially in 2002 and 2003, the early part of the migration season featured relatively long periods of nearly constant flow. In these years, nonetheless, median travel times for yearling chinook salmon decreased throughout the period, even without change in flow. This result suggests that physiological characteristics of juvenile fish (possibly degree of smoltification) that progress throughout the season might have had more influence on migration rates than flow.

As in Smith et al. (Smith et al. 2002), this observation is supported by the partial fits for a generalized additive model of travel time that included year effects and non-parametric splines for date and flow (Fig. 30). This model indicated that flow had a nearly linear effect on travel time throughout the range of observed flow exposures, but that release date had more influence early in the season, until about the end of April. A generalized additive model using the water travel time index gave essentially the same information.

Survival and mortality vs. water travel time

Smith et al (2002) found that the relationship between flow exposure and survival of yearling chinook salmon within seasons was generally weak and inconsistent. Translating the flow exposure measures into a water travel time (WTT) index resulted in qualitatively similar results (Fig. 31. Significant (α=0.05) negative slopes (increased WTT related to decreased survival) occurred for data within the 1998, 2000, and 2003 seasons; the R^2 was 35%, in 2003, and 11% in the other two years. Results in 2001 depended on whether the analysis was weighted according the relative precision of the estimates.

Including all years in an unweighted analysis resulted in a significant regression (Fig. 32). Data from 2001 were highly influential in this result; excluding 2001 data there is a slight negative slope, but it is not significant and there is no predictive value (see sections below on threshold models and discussion of 2001).

For years other than 2001, estimated mortality per day tended to decrease with increasing water travel time (bottom panel, Fig. 33). Data from 2001 stood apart from data from other years (top panel, Fig. 33) and appeared to indicate two distinct sets of release groups. See below for discussion of this pattern.

Threshold models for survival vs. flow

The equation for the best-fit Boltzmann curve (Fig. 34) was as follows:

$$SURV = \frac{0.7854}{1 + e^{(48.13 - F)/9.72}}$$

with R^2= 10.5%. The best-fit broken stick was almost identical to the Boltzmann curve (Fig. 34). The threshold flow exposure value was 73.0 kcfs; maximum survival was 0.777, and the linear equation for survival below the threshold was:

$$SURV = -0.2954 + 0.0147F.$$

Bootstrap 95% confidence intervals on the estimated parameters are as follows: maximum survival: (0.752,0.835); slope: (0.0053,0.0181); threshold: (70.1, 99.4).

It is important to note that the threshold models cannot be fit without the low-flow, low-survival points from 2001. It is those points that “pull down” the curve or line in the low-flow range. Further, the individual points from 2001 don’t fit the curves very well. Taken as a whole, the points from 2001 are effectively acting as a single “center of gravity” or almost as a single point, and within-season dynamics are lost.

Snake River steelhead

Travel time vs. flow and water travel time

With the exception of the low flow year of 2001, the annual median travel time (days) for all Snake River steelhead passing between Lower Granite and Bonneville Dams from 1 April to 31 May each year varied by only a few days (Table 31.)

Table 31. Median travel time (days) of PIT-tagged steelhead between Lower Granite Dam (LGR) and Bonneville Dam (BON), 1995-2003.

Year	Median LGR-BON travel time (days)
1995	20.2
1996	15.3
1997	12.2
1998	14.4
1999	15.4
2000	13.6
2001	29.8
2002	18.4
2003	15.4

Within seasons, median travel time for groups of PIT-tagged steelhead has consistently tracked the water travel time index (Fig. 35). Results from a generalized additive model (including year effects, and non-parametric splines for date and flow exposure index) indicated that date also had an influence on travel time for steelhead (Fig. 36), but less influence than flow. Unlike the result for yearling chinook salmon, flow appeared to have more influence than date on steelhead travel time throughout the migration season. A generalized additive model using the water travel time index gave essentially the same information.

Survival and mortality vs. water travel time

Smith et al. (2002) found that the relationship between flow exposure and survival of steelhead within seasons was generally weak and inconsistent. Translating the flow exposure measures into a water travel time (WTT) index resulted in qualitatively similar results (Fig. 37). Significant (α=0.05) negative slopes (increased WTT related to decreased survival) occurred for data within the 1995, 1999, and 2000 seasons; the R^2 values were 16%, 21%, and 51%,respectively.

Including all years in an unweighted analysis resulted in a significant regression (Fig. 38). As with yearling chinook salmon, data from 2001 were highly influential in this result, and the 2001 data don't fit the line well at all (there are substantial problems with residuals). Excluding 2001 data there is a slight and significant negative slope, but there is little predictive value (see sections below on threshold models and discussion of 2001).

For years other than 2001, estimated mortality per day was fairly constant, regardless of water travel time (bottom panel, Fig. 39). This indicates that the observed relationship between water travel time and steelhead travel time induces in a relationship between water travel time and steelhead survival. Data from 2001 clearly stood apart from data from other years (top panel, Fig. 39). The "baseline" mortality per day appeared to be higher and, contrary to the more constant pattern for other years, the estimated mortality per day decreased with increasing water travel time.

Threshold models for survival vs. flow

The equation for the best-fit Boltzmann curve (Fig. 40) was as follows:

$$SURV = \frac{0.7728}{1 + e^{(59.48 - F)/18.64}}$$

with R^2= 10.2%. In the best-fit broken stick (Fig. 40) the threshold flow exposure value was 115.4 kcfs; maximum survival was 0.779, and the linear equation for survival below the threshold was:

$$SURV = 0.0316 + 0.0065F.$$

Bootstrap 95% confidence intervals on the estimated parameters are as follows: maximum survival: (0.693,0.849); slope: (0.0046,0.0202); threshold: (78.9, 132.6).

It is important to note that the threshold models cannot be fit without the low-flow, low-survival points from 2001. It is those points that "pull down" the curve or line in the low-flow range. Further, the individual points from 2001 don't fit the curves very well. Taken as a whole, the points from 2001 are effectively acting as a single "center of gravity" or almost as a single point, and within-season dynamics are lost.

Subyearling chinook salmon

Flow, Temperature, and Migration Timing

Snake River fall chinook salmon do not have a directed migration as do spring chinook. Some percentage chose not to migrate until after water temperatures cool in September, while some do not migrate until the next spring. From the population of fish PIT-tagged between 1995 and 2000, 46,773 fish were detected passing either Lower Granite, Little Goose, or Lower Monumental Dam prior to 1 September of each year, while 5,301 were detected after 1 September. Of these, those that migrated early produced 142 adult returns, while those that migrated late produced 73, for comparative SARs of 0.32 and 1.29% respectively. Of all fish we PIT tagged over this time period, nearly two-thirds were not detected. Based on CJS survival methodologies, we suspect a large number died before ever reaching Lower Granite Dam. For fish detected the first time after 1 September, we do not know what proportion of the population the live fish represented. Certainly, they came from some large population.

Flow/travel Time Estimates

Summer-migrating subyearling fall chinook salmon have a much more complex migration pattern than spring-migrating salmonids, thus, results from PIT-tag studies do not fall into neat, discrete parts. Most data on fall chinook survival come from studies conducted above Lower Granite Dam. Since 1992, Connor et al. (2003a) have beach seined, PIT-tagged, and released fall wild chinook in their rearing areas. Since 1995, NOAA Fisheries has also PIT-tagged subyearling fall chinook at Lyons Ferry Hatchery, trucked them upstream above Lower Granite Dam, and released them at a time and size to match wild subyearling fall chinook salmon in their rearing areas (Smith 2003). As travel time to the Lower Granite Dam typically averages one month or more from time of release after tagging, survival estimates to Lower Granite Dam, represent survival during both rearing and migration (Connor et al. 2003a; Connor et al. 2003b; Smith 2003). Subyearling fall chinook salmon rear and develop physiologically as they migrate, and their migration rate increases with migration distance and increased size. Unlike yearling smolts that generally all migrate quickly to Lower Granite Dam, some fall chinook don't for months. Thus, standard techniques used for yearling smolts to measure travel times or survival don't work quite as well. From 1995 to 2000, we released nearly 200,000 PIT-tagged smolts above Lower Granite Dam. Subsequently we detected only about 62,000. Of these nearly 15% were not detected at a Snake River dam until after 1 September of the year, some not until the following spring.

For the "active" migrants, those that passed the Snake River dams in June, July, and August in the year of release for the hatchery fish, the median pooled travel time for all years from release to detection at Lower Granite Dam averaged 43.5 days (Smith 2003). Within each migration year, median migration rate between each pair of dams was substantially greater between Lower Monumental and McNary Dams and between McNary and Bonneville Dams than between pairs of dams upstream from Lower Monumental Dam.

Juvenile fall chinook salmon historically moved out of the upper Snake River spawning and rearing areas in late March/early April. The peak of the run had passed Ice Harbor Dam by mid-June. The construction of the three dams in Hells Canyon substantially altered conditions for migrant fish. Thus, little in the migration of juvenile fall chinook salmon under present conditions matches the historic run timing of the fish.

Discussion

As a consequence of FCRPS dam construction on the mainstem of the lower Snake and Columbia Rivers, the average travel time of yearling chinook salmon and steelhead migrating between the confluence of the Clearwater and Snake Rivers to the lower river below Bonneville Dam has increased substantially. As a result, for smolts left in river to migrate, their timing of arrival to the estuary and nearshore ocean is delayed on average by several weeks. As discussed in the section on transportation, timing of ocean entry can greatly affect SARs. Coupled with the declining lipid reserves in migrating yearling chinook salmon observed by Congelton et al. (2004), fish arrive to the estuary later and likely with lower energy reserves than they did prior to completion of the FCRPS, and even more so in low flow years. Thus, although little relationship was found between flow and survival in the Snake River, it seems reasonable that in can affect their survival below the hydropower system, although its more difficult to measure. Furthermore, as a consequence of construction of the FCRPS, spring-time flows and turbidity have been greatly reduced, which likely increases the vulnerability of smolts to predators upon ocean entry.

In addition, as identified in the section on juvenile reach survival, it appears that as migration times for steelhead increase, the percentage of the population that continues to migrate decreases. This leads to lower estimates of survival.

Regarding spring migrants from the Snake River (steelhead and yearling chinook salmon), conclusions regarding the influence of the river environment on travel time and survival depend in very large part on the interpretation of information from the low-flow year 2001. Data from that year are highly influential (or outliers) in multi-year analyses of the influences of flow (c.f. Figs. 32, 33, 38, and 39). Threshold models for survival vs. flow exposure cannot even be estimated without including the low-flow data along with the more moderate-to-high flow data from other years.

The cases where 2001 data don't fit the multi-year trends (e.g., positive slope between water travel time and estimated survival for steelhead within 2001; apparent occurrence of two distinct sets of release groups of yearling chinook salmon) should lead to closer examination of patterns of mortality in 2001. The greatest water travel times (lowest flow volumes) in the entire data set occurred at the beginning and end of 2001 (top and middle panels, Fig. 41). Both the highest and lowest yearling chinook salmon survival of 2001 occurred during these periods, which caused the two distinct sets of points (e.g, Fig. 41). Survival during the peak flows of 2001 was no higher than in the low flows at the beginning of the season. The "missing variable" is water temperature (bottom panel, Fig. 41). In the entire data set of 458 yearling chinook salmon release groups, only 13 experienced temperature exposures greater than 15°. Of these, 12 occurred at the end of the 2001 season.

The 2001 data is crucial to fitting models of flow and survival to data points from 1995 through 2003. This is especially true for the specific threshold models included here, but would be equally true, for example, in data sets that use different groupings (say weekly) at Lower Granite Dam. The 2001 data tends to function much like a single point in such multi-year analyses, particularly the "anchor points" of low survival late in 2001. More work is needed to determine how much of the apparent low-flow effect is actually an effect of lethal temperatures or lack of spill at dams.

Because it is tempting to interpret the threshold models as a prescription for a certain amount of flow, it is crucial to note the extreme imprecision in the the estimates of the break points. The estimated breakpoint for Snake River yearling chinook salmon was 73.0 kcfs, but bootstrap methods were used to calculate a 95% confidence interval of 70.1 to 99.4. For Snake river steelhead, the situation was even worse: the point estimate was 115.4 kcfs, but we reach 95% confidence in our interval only if it as wide as somewhere between 78.9 and 132.6 kcfs. We know that salmonid survival will approach zero if flow is at zero, and we know that survival was lower in low-flow 2001 than the more constant survival levels we've seen with moderate to high flow. But the current data give almost no information for establishing an exact threshold above which survival is "as high as it can get" and below which survival drops off more or less steeply.

LATENT MORTALITY ASSOCIATED WITH THE FCRPS

For stocks of fish upstream of the FCRPS, the survival rate of juvenile fish downstream of Bonneville Dam in most cases determines the subsequent fate for different stocks. Except in low-flow years, as detailed in the "Juvenile reach survival estimates" section above, for most of these stocks, direct juvenile fish survival within the hydropower system is now as high or higher than existed during the 1960s when the FCRPS consisted of only 4 mainstem dams on the lower Snake and Columbia Rivers. Further, fish collected at upstream dams and transported to a release site below Bonneville Dam survive to release at an estimated 98% or higher rate. Nonetheless, with the exception of some adult return rates for some stocks in the last couple of years, overall adult return rates of fish have rarely approached estimated return rates from the 1950s and1960s. Thus, considerable effort has gone into studies and analyses to explain or determine why the adult return rates have differed. At the ends of the spectrum, mechanisms to explain the differences in adult return rates range from entirely to changes in ocean conditions to "delayed" affects on juveniles as a result of their passage history through the hydropower system.

In a general sense, "delayed" mortality is any mortality that occurs as the result of some event that is not expressed until after the event has occurred. This contrasts to direct mortality that occurs associated with an event, such as, death from mechanical injury while passing through a turbine. "Delayed" mortality associated with the FCRPS might result from changes in migration timing, injuries or stress incurred during migration through juvenile bypass systems, turbines, or spill at dams that does not cause direct mortality, disease transmission or stress resulting from the artificial concentration of fish in bypass systems or barges, depletion of energy reserves from prolonged migration, gas bubble trauma, altered conditions in the estuary and plume as a result of FCRPS construction or operation, and disrupted homing mechanisms. Because, by definition, "delayed" mortality occurs after fish have arrived below Bonneville Dam, and it generally occurs beyond where juvenile sampling occurs, we lack bodies of dead fish or samples that might provide indications of the extent that hydropower system passage causes the mortality.

To this point, we have used the term "delayed" mortality to cover all mortality of juveniles downstream of Bonneville Dam. In the case of "delayed" mortality associated with the FCRPS, this broad term encompasses other definitions used in the past: "delayed" mortality, "extra" mortality, and "D", all of which have a specific definitions, but sometimes have been used interchangeably. Here, we first clarify past terminology, then relate it the term we define as latent mortality associated with the FCRPS. In the broadest sense, latent mortality represents all anthropogenic mortality for juveniles downstream of Bonneville Dam prior to adult return. It could result from different juvenile histories associated with hydropower system passage, impacts from hatchery practices, or changes in the ocean predator/prey ecosystem due to ocean harvests on non-salmonid stocks. We confine, however, our discussions to latent mortality associated with the FCRPS.

Extra mortality is a term that arose in the PATH process. Marmorek et al. (2001)defined extra mortality as:

> any mortality occurring outside of the juvenile migration corridor that is not accounted for by either: 1) productivity parameters in spawner-recruit relationships; 2) estimates of direct mortality within the migratory corridor (from passage models); or 3) for the delta model only, common year effects affecting both Snake River and Columbia River stocks. Extra mortality can in theory occur either before or after the hydropower migration corridor.

Thus, extra mortality is purely a modeling construct. Further, several hypotheses, including hydropower effects, were proposed in PATH to explain extra mortality. Thus, extra mortality is not synonymous with latent mortality related to the hydropower system. For this reason, we do not use the term "extra" mortality (a modeling construct) to describe hydropower system-related latent mortality.

Another source of confusion arises from the relationship between D and "delayed" mortality associated with in-river migrants. D refers to the ratio of smolt-to-adult survival (measured from below Bonneville Dam to Lower Granite Dam) of transported fish relative to that of in-river migrants. Because D is typically below 1.0 for Snake River spring/summer chinook and steelhead, it leads to a latent mortality for transported fish. This latent mortality may result from stress experienced on the barge, disruption of timing to the estuary, or increased straying or fallback of adult migrants. While we lack specific mechanisms that lead to D < 1.0, we can directly quantity D as it relates to the SARs for in-river migrants. Of course, the SAR for in-river migrants includes any hydropower-related latent mortality, so the magnitude of D is dependent on the magnitude of latent mortality of in-river migrants. Thus, D is not a direct measure of the latent mortality of transported fish because if we could decrease the magnitude of hydropower-related latent mortality of in-river migrants, we would in effect increase the value of D.

To standardize the discussion, we use the following notation (Fig. 42). First, we designate survival as S and mortality (1 - S) as μ. In-river migrants are denoted by the subscript I, and transported fish are designated by the subscript T. We partition survival and mortality into the following life stages: downstream migration through the hydropower system (ds), estuary/ocean (e/o), and upstream migration through the hydropower system (us). We further partition the estuary/ocean stage to reflect survival that would occur in the absence of the hydropower system ($S_{e/o}$) and hydropower system-related latent mortality (subscript δ), which applies to both transported fish and in-river migrants). Thus SAR of in-river and transported fish is expressed as:

$$SAR_I = S_{I,ds} \cdot S_{e/o} \cdot (1 - \mu_{I,\delta}) \cdot S_{I,us}$$
$$SAR_T = S_{T,ds} \cdot S_{e/o} \cdot (1 - \mu_{T,\delta}) \cdot S_{T,us}$$

Note that we use the same natural saltwater survival for both in-river and transported fish. This is the survival fish would experience in the absence of dams. Also, we use separate upstream survival for in-river and transported fish. Based on the equations above, we calculate D as:

$$D = \frac{(1 - \mu_{T,\delta}) \cdot S_{T,us}}{(1 - \mu_{I,\delta}) \cdot S_{I,us}}$$

Note that part of the magnitude of D is accounted for by the differential upstream survival of transported and in-river migrating fish.

The rest of this discussion will focus on latent mortality of in-river migrants associated with their passage through the hydropower system, which we refer to as $\mu_{I,\delta}$. Since this type of mortality is important to assessing the effects of the hydropower system on salmonid stocks, and since it is very difficult to ascertain, it is a controversial topic. But we can say that if we removed all the dams, we would also remove the mortality $\mu_{I,\text{ټ}}$ Unfortunately, this also points to the only feasible way to directly measure $\mu_{I,\text{ټ}}$ – a controlled experiment where the control is a river with all dams in place and a treatment where all dams are removed. Clearly this is unlikely, so we are left with indirect inference.

Efforts to Quantify the Magnitude of Latent Mortality

As just mentioned, quantifying the magnitude of latent mortality (for either transported or in-river migrants) is extremely difficult. This is primarily because no suitable control exists. Several methods have been explored to overcome this shortcoming, and here we discuss several.

Upstream/downstream comparisons

Several studies (Deriso et al. 2001; Marmorek et al. 1998a; Schaller et al. 1999)have used downstream stocks (e.g., spring chinook from the John Day River basin) as controls for upstream stocks (e.g., spring-summer chinook from the Snake River basin). While we believe that analyses of the co-variability of populations are inherently interesting, we also believe it is extremely difficult to ascribe differences in variability among stocks to particular factors particularly those that represent a relatively small proportion of the entire life cycle (such as migration through the hydropower system). Below we provide several lines of reasoning in support of this belief.

Salmon Biology

Salmon populations are notorious for their local adaptation (Hendry et al. 2000; Ricker 1972; Taylor 1991; Unwin and Glova 1997)and this had led to extreme biodiversity among populations (Hilborn et al. 2003). Even within salmon populations, a diversity of life-history strategies are supported, and differential growth opportunities between freshwater and saltwater habitats along with cost of migration are believed to be factors that contributes to the selection of life-history traits (Gross 1987; Gross et al. 1988; Randall et al. 1987; Taylor 1990). Further, the upstream/downstream comparison assumes that the major source of environmentally-induced variability in salmon productivity arises from ocean conditions, and since the upstream stocks share a common ocean habitat, they should show high levels of co-variability. However, Bradford (Bradford 1995)concluded that across all of the species he analyzed, the freshwater environment contributes more to variability in egg to adult survival than the ocean. Further, since freshwater survival rates are uncorrelated among salmon populations more than a few hundred km apart (Myers et al. 1997), we must assume that poor correlation in freshwater survival exists between upstream and downstream stocks. Given all this, it is not surprising that salmon populations from distinct regions respond differently to large scale climate patterns (Levin 2003)or that poor correlation exists between patterns of productivity of upstream and downstream stocks (Botsford and Paulsen 2000).

Modeling issues

All the analyses listed above relied on models, and we must recognize that using models that are potentially mis-specified brings in another source of uncertainty. All the analyses assumed, without testing, that the Ricker model appropriately described the population dynamics of the analyzed populations. In fact, the Ricker model is often rejected when compared to simpler models in the Snake River stocks (Zabel and Levin 2002). Further, the spawner and recruit "data" represent models that require several assumptions, and the potential multiplication of errors associated with the stock reconstructions can potentially lead to unidentified bias. One assumption in particular might account for much of the temporal differences between upstream and downstream stocks. In the run reconstructions for PATH, values used for adult survival generally ranged from 40 to 60% through 8 dams (Marmorek et al. 1998a). Recent data from PIT tags suggests the survival greater than 85% for yearling chinook salmon (see Table 10a). Thus, when we consider pre- and post-dam periods, this inflation of dam mortality results in an inflation of the upstream-downstream differences attributed to latent mortality. Further, the models used in the analyses generally ignored differential environmental effects that occurred in several distinct life stages, particularly those associated with freshwater spawning and rearing.

Data issues

Data quality problems exacerbate the problems cited above. Past spawner counts were notoriously noisy because of the high degree of sampling error (Holmes 2001). This leads to limited power to detect effects with these data (Hinrichsen 2001). Thus, problems exist when using these data to measure the magnitude of latent mortality. Further, unequal data quality exists among populations. The John Day populations, in particular, suffer from a lack of age composition data in early years. Zabel and Levin (Zabel and Levin 2002)demonstrated that the practice of applying mean-age compositions to returning adults in run reconstruction leads to severe biases in estimated stock-recruit model parameters.

When all these sources of uncertainty are taken into account, we believe that the uncertainty about any estimate of hydropower-related latent mortality using upstream/downstream comparisons is so large as to render these estimates misleading and essentially useless.

Multiply-bypassed fish

Another source of evidence for latent mortality of in-river migrants relates to observations that in some years and for some stocks multiply-bypassed fish returned at lower rates than fish that were never detected in a bypass system (Sandford and Smith 2002). Most data from the 1995 through 1998 outmigrations indicated that multiply-bypassed spring-summer chinook salmon and hatchery steelhead had lower SARs than those not detected at collector dams (Figs. 43 and 44.) Budy et al.(2002)claimed this was direct evidence that fish passing through bypass systems suffered "delayed" mortality associated with this passage. However, more recent data from the 1999 and 2000 outmigrations did not find differential SARs for wild steelhead or wild chinook salmon (Figs. 43 and 44). Low sample sizes may have attributed to early findings. Further, we present in the "Selective Mortality" section below data that suggest a mechanistic reason for the differences in adult returns unrelated to bypass system history. In summary, we have found that bypasses clearly have selected for smaller fish, and that smaller fish generally return at lower rates than larger fish. Thus, we reasonably assume that multiply bypassed fish are, on average, smaller than non-bypassed ones and should return at lower rates. These observations do not necessarily nullify the Budy et al.(2002) hypothesis, but they do present an alternative and plausible explanation for the data.

Disrupted timing

The construction of the hydropower system has resulted in the extension of travel times of downstream migrants. (Zabel and Williams 2002)observed that for 1 out of 2 years they analyzed, in-river migrants that migrated earlier in the season returned at higher rates than later migrants. This pattern is borne out in 2 of the 3 years analyzed since then (see "Selective Mortality" section below). Thus, we believe that delayed entry into the estuary has resulted in lower return rates, which is a form of latent mortality associated with passage through the hydropower system. More detailed analyses with more years of data hold promise to estimate the magnitude of this effect. Similarly, transportation of fish, particularly early in the season, delivers fish below Bonneville Dam earlier than they would have arrived had they migrated through a free-flowing river. We believe this has also contributed to poorer than expected return rates, which, again, is a form of latent mortality.

Latent mortality of transported fish

We feel the strongest evidence for some form of latent mortality is that estimates of D are consistently well below 1.0 for all Snake River ESUs. Since transported fish return from below Bonneville at substantially lower rates than in-river migrants, they must suffer from some form of latent mortality. Regardless of the cause – timing issues, greater susceptibility to predation, disease or stress due to crowding, or problems with homing – transported fish incur mortality as a result of transportation that isn't expressed until after the fish are released from the barges.

Discussion

When we considered all the evidence presented above, it seems clear that latent mortality exists. However, we have very limited capability to precisely estimate the overall magnitude of hydropower system-related, latent mortality for either transported fish or in-river migrants. Certainly, we have much stronger evidence for substantial latent mortality of transported fish (see values of D in "Transportation Evaluations" section). In terms of in-river migrants, it appears reasonable to assume that some latent mortality exists. Perhaps the strongest support for this rests on likely disruption of historical migration-timing patterns. However, the recent return rates of wild fish implies that hydropower system-related latent mortality is not such an overwhelming force that it will prevent stocks from returning to abundances observed before the hydropower system was completed. This is not to say that recent return rates could not have been even higher – we have no evidence for this one way or another. Another plausible hypothesis is that latent mortality is greater during poor ocean conditions. Our observation that length-related, selective mortality appears related to ocean conditions supports this hypothesis. However, little other evidence supports or refutes this hypothesis. So, we are left with the rather unsatisfying conclusion that for in-river migrants, hydropower system-related, latent mortality falls somewhere in the range of very weak to strong and that we have little hope to discern among this broad range of alternatives.

SELECTIVE MORTALITY

As indicated in the section above, numerous factors could impact SARs. Some recent efforts by Zabel and Williams (2002)determined that size and timing of fish within populations influenced SARs. In this section we expand upon results presented by Zabel and Williams (2002).

The first step in the analysis involved calculating the directional selection coefficient (Endler 1986), which for a trait *x* is defined as:

$$\delta = \frac{\overline{x}_R - \overline{x}_T}{\sqrt{\mathrm{var}_T}}$$

where $\overline{X}$ is the mean value of the trait in the entire tagged population (*T*) and in returning adults (*R*). Note that the returning adults represented a sub-population of the entire tagged population, and we refer to their traits at the time of tagging. If the trait is length, for instance, then a positive value of δ means that larger fish returned at a higher rate than smaller ones. We performed a Monte Carlo test (see (Zabel and Williams 2002)for details) to determine whether the selection coefficient was significantly different from zero.

In the top plot of Fig. 45, points above the horizontal dashed line indicated that larger fish returned at greater rates than smaller ones. In the bottom plot, points below the line indicated that earlier migrants returned at greater rates than later migrants, and the opposite held true for points above the line.

When we updated the results from Zabel and Williams (2002) by adding more years (1998 through 2000 for Snake River spring-summer chinook) and Snake River steelhead for 1999 and 2000, the main conclusions still held: the size of individuals and the timing of their outmigration strongly influenced return rates. Selectivity mortality based on fish length was generally not as strong in 1998 through 2000 as it was in 1995 and 1996 for spring-summer chinook salmon (perhaps due to better ocean conditions), although the level of length-based selective mortality was similar across years for transported wild fish (Figure 45, Table 32). For the two years of data on return rates of steelhead, we observed strong length-based selective mortality, with all groups of steelhead incurring greater selective mortality than their chinook counterparts (Figure 45, Table 32). In-river spring-summer chinook migrants early in the season typically returned at higher rates as demonstrated by negative selection coefficients ($P < 0.05$ for 4 out of 5 years for wild fish and 3 out of 5 for hatchery fish, Table 33). While the magnitude of timing-based selection varied yearly for in-river migrants, the pattern of variability was consistent among hatchery and wild chinook and steelhead, with strong selection in 1995, 1998, and 2000 and weaker selection in 1995 and 1999 (Figure 45, bottom plot). Timing-based selection was variable for transported fish, with fish transported early in the season returning at higher rates in some years, and fish transported later returning at higher in other years. Also, there was little consistency between wild and hatchery chinook salmon.

Table 32. Sample size (N), mean length (mm) at tagging (standard error in parentheses) for the total tagged population and returning adults of Snake River spring-summer chinook salmon and steelhead PIT tagged at Lower Granite Dam. δ is the selection coefficient (see text), and the P-value is based on a Monte Carlo test to determine if is greater than zero. If $P < 0.05$, then δ is significantly greater than zero at the $\alpha = 0.05$ level.

Release group	Total population		Returning adults		percent return	δ	P-value
	N	Mean length (s.e.)	N	Mean length (s.e.)			
Snake River spring/summer chinook salmon							
1995							
In-river W	5331	107.37 (0.11)	5	113.80 (3.44)	0.094	0.790	0.039
In-river H	21,596	136.55 (0.12)	62	143.95 (2.20)	0.287	0.422	0.001
Transport W	3369	106.84 (0.14)	12	110.17 (2.87)	0.356	0.409	0.079
Transport H	15,583	136.17 (0.14)	93	141.62 (1.30)	0.597	0.315	0.002
1996							
In-river W	13,92	109.31 (0.07)	7	115.00 (1.83)	0.050	0.741	0.023
In-river H	53,420	139.45 (0.06)	53	146.59 (2.31)	0.099	0.479	0.001
Transport W	8656	110.49 (0.08)	10	113.00 (1.50)	0.116	0.351	0.139
Transport H	36,867	139.62 (0.07)	53	146.30 (2.14)	0.144	0.477	0.001
1998							
In-river W	8676	113.01 (0.07)	53	113.75 (0.82)	0.611	0.115	0.208
In-river H	61,541	135.72 (0.05)	229	135.43 (0.75)	0.372	-0.025	0.643
Transport W	5476	111.97 (0.09)	33	114.09 (1.13)	0.603	0.306	0.036
Transport H	38,773	135.95 (0.06)	243	136.73 (0.67)	0.627	0.062	0.169
1999							
In-river W	11,827	109.38 (0.08)	152	110.20 (0.58)	1.285	0.099	0.106
In-river H	61,491	137.82 (0.05)	891	139.29 (0.43)	1.449	0.114	0.001
Transport W	8,113	109.43 (0.09)	172	111.05 (0.56)	2.120	0.196	0.004
Transport H	43,169	138.16 (0.06)	866	138.71 (0.37)	2.006	0.042	0.110
2000							
In-river W	42,899	110.38 (0.03)	605	111.37 (0.27)	1.410	0.139	0.000
Transport W	15414	109.77 (0.06)	261	111.41 (0.43)	1.693	0.228	0.000

Table 32, continued;

Snake River Steelhead							
1999							
In-river W	8338	186.36 (0.30)	64	200.80 (3.68)	0.768	0.528	< 0.001
In-river H	59,487	218.78 (0.10)	380	224.81 (1.25)	0.639	0.253	< 0.001
Transport W	5853	186.56 (0.35)	82	204.66 (3.06)	1.401	0.672	< 0.001
Transport H	40,525	219.61 (0.12)	439	227.60 (1.11)	1.083	0.333	< 0.001
2000							
In-river W	47,998	184.69 (0.13)	936	201.72 (1.11)	1.950	0.602	< 0.001
Transport W	22,212	183.77 (0.18)	959	192.70 (0.95)	4.317	0.331	< 0.001

Table 33. Sample size (*N*), mean release day of the year (standard error in parentheses) for the total tagged population and returning adults of Snake River spring/summer chinook salmon and steelhead PIT tagged at Lower Granite Dam. δ is the selection coefficient (see text), and the *P*-value is based on a Monte Carlo test to determine if is greater than or less than zero. If $P <$ 0.05, then δ is significantly greater or less than zero at the $\alpha = 0.05$ level.

Release group	Total population		Returning adults		percent return	δ	*P*-value (2-tailed)
	N	Mean rls date (se)	*N*	Mean rls date (se)			
Snake River spring/summer chinook salmon							
1995							
In-river W	31,766	119.81 (0.10)	63	114.81 (1.94)	0.198	-0.290	0.007
In-river H	104,279	121.06 (0.03)	321	118.42 (0.43)	0.308	-0.268	0.000
Transport W	21,359	119.84 (0.10)	78	125.77 (2.07)	0.365	0.410	0.000
Transport H	81,780	120.95 (0.03)	455	122.29 (0.40)	0.556	0.143	0.001
1996							
In-river W	14,078	117.62 (0.09)	7	116.43 (4.27)	0.050	-0.112	0.427
In-river H	53,976	126.52 (0.04)	53	126.23 (1.97)	0.098	-0.030	0.416
Transport W	8699	117.80 (0.11)	10	114.5 (2.62)	0.115	-0.314	0.167
Transport H	37,027	126.09 (0.05)	53	125.68 (1.41)	0.143	-0.042	0.382
1998							
In-river W	8,714	111.93 (0.13)	53	103.79 (1.14)	0.608	-0.687	< 0.001
In-river H	61,853	114.55 (0.04)	230	109.17 (0.61)	0.372	-0.481	< 0.001
Transport W	5,496	111.83 (0.16)	34	106.09 (1.44)	0.619	-0.499	< 0.001
Transport H	39,032	114.96 (0.06)	245	116.86 (0.68)	0.628	0.174	0.004
1999							
In-river W	11,853	118.79 (0.13)	152	116.65 (0.73)	1.282	-0.148	0.029
In-river H	61,742	121.88 (0.04)	892	121.67 (0.29)	1.445	-0.023	0.242
Transport W	8128	119.88 (0.14)	172	121.11 (0.75)	2.116	0.098	0.101
Transport H	43,305	122.74 (0.04)	867	125.37 (0.27)	2.002	0.296	< 0.001
2000							
In-river W	43,241	124.55 (0.08)	610	119.29 (0.51)	1.411	-0.331	< 0.001
Transport W	15,535	120.37 (0.13)	261	118.97 (0.89)	1.680	-0.087	0.078

Table 33, continued;

Snake River Steelhead							
1999							
In-river W	8361	124.41 (0.16)	64	124.08 (1.73)	0.765	-0.022	0.431
In-river H	59,759	128.26 (0.05)	381	125.16 (0.56)	0.638	-0.234	< 0.001
Transport W	5872	126.40 (0.19)	83	127.40 (1.31)	1.413	0.069	0.263
Transport H	40,771	128.29 (0.06)	442	130.00 (0.53)	1.084	0.134	0.003
2000							
In-river W	48,357	117.22 (0.05)	941	112.02 (0.24)	1.946	-0.467	< 0.001
Transport W	22,360	113.00 (0.06)	964	113.45 (0.26)	4.311	0.049	0.059

DISCUSSION

In this general discussion section, we consider some important issues that did not fit into the major topics presented above. We also discuss some issues that tie together conclusions from several sections.

Large-Scale Processes

Increasing evidence points to dramatic changes in the marine ecosystem of the northern Pacific Ocean over the past 2000 years resulting from shifts in climate (Finney et al. 2002; Moore et al. 2002). Throughout this region, variations in zooplankton, benthic invertebrates, seabirds, and fish have all been connected to changes in ocean-climate conditions (McGowan et al. 1998). In particular, analyses of data from the last 100 years demonstrate a strong influence of ocean conditions on catches and the production of Pacific salmon (*Oncorhynchus* spp.) across a range of spatial and temporal scales (Beamish et al. 1999; Mantua et al. 1997). The varied response of salmon to past environmental changes likely reflects their complex life history strategies and the wide diversity of freshwater and marine habitats that they occupy (Hilborn et al. 2003).

Recent analyses suggest that chinook salmon from the Columbia River basin also respond to cyclic changes in ocean-climate conditions. Modeling exercises directed at explaining the negative effects of various anthropogenic activities on the productivity of Snake River spring/summer chinook salmon identified the estuary and ocean environments as important sources of unexplained variation in stock performance (Kareiva et al. 2000; Wilson 2003). Using catch records from commercial fisheries, Botsford and Lawrence (2002) found reasonable correlations between the inferred survival of Columbia River chinook salmon and physical attributes of the ocean, such as sea-surface temperature and coastal upwelling. Building upon these previous studies, Scheuerell and Williams (In review) found that they could actually forecast changes in the smolt-to-adult survival of SRSS chinook from changes in coastal ocean upwelling over the past 37 years, including the rapid decline between the 1960s and 1970s and the increase in the late 1990s (Fig. 46.) All of these analyses highlight the important effects of the ocean in determining smolt-to-adult survival, and further support Pearcy's (1992) assertion that the primary influence of the ocean on salmon survival occurs early within the first year that juveniles occupy coastal waters.

The climate processes that affect the ocean's physical environment, and thereby influence salmon growth and survival, also affect climate patterns in rainfall and temperature on the continental land masses (Coulibaly and Burn 2004; Rodionov and Assel 2003). For instance, during time periods of relatively poor ocean conditions for Columbia River salmon, such as those indicated by a positive phase of the Pacific Decadal Oscillation (PDO, Mantua et al. 1997), we also observe below-average river flows in the Columbia River basin (Fig. 47), suggesting additional negative effects on salmon populations (reviewed by Budy et al. 2002). We note also that the highest salmon catches in the Columbia River occurred during the 1880s, coinciding with the period of the highest normalized Columbia River flows in the last 120 years. Several lines of evidence suggest the Northeast Pacific underwent another ocean "regime shift" in 1998(Peterson and Schwing 2003). Already we have witnessed improved smolt-to-adult survival and subsequent adult returns in recent years, suggesting a positive switch in the environmental conditions that favor salmon growth and survival. Assuming these patterns in ocean and continental climate hold, salmon populations in the Pacific Northwest should continue to respond favorably until they switch again. Concentrating more effort on forecasting changes in salmon responses to future climate change and negative anthropogenic activities should help us to better manage Columbia River salmon and avoid the massive losses incurred during the last period of poor climate conditions.

Diversity

Dams have become major selective forces on migratory salmonid populations by dramatically changing environmental conditions in the migratory corridor, including reducing river velocities, blocking spawning areas, and fostering altered biotic communities. An extreme example of this is Snake River fall chinook. Historically, most Snake River fall chinook spawned above the Hells Canyon Dam complex; now the entire ESU spawns below Hells Canyon in a much altered temperature regime (Ebel 1968). Further, it is likely that in the pre-impoundment era, most ocean-type chinook fry in the Columbia River Basin were swept by spring flows to the estuary (Mains and Smith 1964; Park 1969) where most of their juvenile rearing occurred. In the current river configuration, ocean-type chinook salmon originating from the Snake River, Hanford Reach, or Upper Columbia River encounter slack water in impounded reservoirs and hold up to rear to a larger size before continuing to migrate volitionally.

The fact that salmon populations have the capability to evolve rapidly (Hendry et al. 2000) and that we have demonstration strong selective forces on some stocks (see Selective Mortality) suggests Columbia River salmonids will evolve in response to selective pressures created by dams. We do not know the long-term consequences of these selective pressures as they have only acted on populations for 10-15 generations. Thus, while almost all management is focused on actions that will take effect within a generation, we believe it is important to also consider the impacts of management actions on evolutionary time scales. In particular, how will dams and their associated mitigation actions affect the diversity of salmonid populations?

NOAA Fisheries defines a viable salmonid population as "an independent population of any Pacific salmonid (genus *Oncorhynchus*) that has a negligible risk of extinction due to threats from demographic variation, local environmental variation, and genetic diversity changes over a 100-year time frame" (McElhany 2000). Genetic diversity is important because it protects a species by allowing a wider use of environments, protects against short-term spatial and temporal environmental changes, and provides the raw material for surviving long-term environmental change (McElhany 2000). Indeed, Hilborn et al. concluded (2003) that the overall Bristol Bay sockeye salmon populations has remained at a high level specifically due to diversity of populations. Thus, efforts to ensure diversity in listed Columbia River stocks is warranted. To this end, the NOAA Fisheries believes it necessary to "limit or remove human-caused selection or straying that weakens the adaptive fit between salmonid population and its environment or limits a population's ability to respond to natural selection" (McElhany 2000).

Similarly, the Independent Scientific Group recommended that "Because the full assemblage of salmonids in the Columbia River basin probably used many migration strategies", a diversity of management schemes should be used to assist migration. Without diversity of management, there is likely to be further stock selection" (ISG 1996). Fish bypass systems, spillways, the use of transportation, flow augmentation, and other management strategies may select for particular stocks or life histories and could therefore reduce diversity if used exclusively. Therefore, in their review of transportation, the Independent Scientific Advisory Board concluded that "Spreading the risk of negative outcomes among alternative routes of hydroelectric passage is advisable to prevent a recovery action designed for one listed species from becoming a factor in the decline of another species", and "in the face of uncertainties associated with potential negative effects of transportation on genetic and life history diversity"(ISAB 1998).

We concur with these conclusions. In light of this and the material presented previously, we believe particular attention needs to focus on 1) exploration of alternative transportation strategies, including allowing more fish to migrate volitionally, adopting seasonally varying transportation schemes, and considering ways to delay the delivery of early transported migrants to the estuary; 2) the ability of augmentation and spill to speed up downstream migration; 3) consideration of population structure in mitigation actions to determine if actions equally benefit all segments within and between populations; and 4) how anthropogenic changes potentially create selection pressures on fish stocks, e.g., if the unprecedentedly large populations of avian predators select against larger fish.

Hydropower System And Harvest

The estimates of SAR in previous sections were based on escapement + harvest, which provides information on population performance. If we estimate SAR based only on escapement, it provides information on the actual number of spawners entering the Snake River basin above the hydropower system. The escapement-based SAR of spring-summer chinook salmon provides an index of escapement over time. The estimated SARs to the uppermost dam for the last several brood years actually exceeded most of those in the 1960s (Fig. 48.) As depicted in Figure 48, to some degree this resulted from reduced mainstem harvest on the upstream stocks. The data suggest that if ocean conditions that produced the present higher rates of return continue for a few years into the future, absolute adult escapement over Lower Granite could possibly exceed levels observed in the 1960s if harvest rates continue at the current levels.

CONCLUSIONS/SUMMARY

• Our ability to discern FCRPS-related effects is directly related to the quality of data available, which is quite variable. We can precisely estimate survival of downstream migrants from release points to the uppermost dams and through the hydropower system, and we are developing similar capabilities for upstream migrants. For several ESUs, we are developing a general sense of the relative performance of transported fish compared to in-river migrants, but we are somewhat limited by sample sizes of adult returns. Unfortunately, we have limited ability to quantify the magnitude of hydropower system-related, latent mortality. However, we believe a major component of latent mortality is the disruption of timing of transported fish and in-river migrants, and we are beginning to discern some migrational timing effects.

• Areas where additional or continued study would help resolve some uncertainties about effects of the FCRPS include: 1) migrational timing and its affect on SARs for both transported and in-river migrants, 2) selectivity of bypass systems, for fish size as well as fish health, and 3) mechanisms leading toward latent mortality.

• Part of the data limitations discussed above arise from the fact that probably the best indicator of population performance is adult return rate, but this measure reflects the effects of several confounding factors, one of which is effects related to FCRPS. It is clear, though, that ocean conditions are the dominating factor in determining return rates, overriding variability associated with the hydropower system. Return rates have increased by an order of magnitude since the recent upturn in ocean conditions while survival through the hydropower system has remained relatively constant. Improvements in SARs, though, do not preclude the existence of hydropower system-related, latent mortality or a latent mortality/ocean condition interaction.

• Transportation is not a panacea. When comparing annual indices of transported versus in-river fish, in many cases, transportation appears to confer little benefit, nor harm. However, under certain times of the year and under conditions of low flow, transportation is very beneficial.

Further, the benefits of transportation decrease as fish are transported from sites closer to Bonneville Dam. Thus, future operations should focus on optimizing the benefits of transportation. Strategies such as "spread the risk" and promotion of diversity suggest we should allow more fish to migrate in the river whenever possible.

• Direct juvenile survival under most conditions for yearling migrants is relatively high, and substantial improvements in downstream survival appear unlikely, particularly improvements related to passage through dams. Summer migrants suffer greater mortality in reservoirs than do spring migrants, and improvements in river conditions may confer considerable survival improvements. The anomalously low survival experienced by spring migrants in 2001 and generally lower survival of summer migrants likely resulted from conditions in the reservoirs, and possibly a lack of spill. Therefore, we feel that we may be facing diminishing returns in terms of improving survival via technological fixes to dams. Efforts to reduce mortality in the reservoirs, obtaining an understanding about how to reduce latent mortality, and maintaining diversity by improving habitat conditions in the estuary and in freshwater spawning/rearing habitats will likely have the most influence on overall stock viability.

• Although we found little or no relationship in the Snake River between flow and survival of spring migrants, flow clearly can affect their migrational timing to the estuary. Arrival timing appeared to greatly influence their SAR. Furthermore, delayed migration reduces available energy reserves in smolts and could affect survival, a condition exacerbated in low flow years, both within the hydropower system, but also in the freshwater areas upstream that fish negotiate prior to arriving at the first dam.

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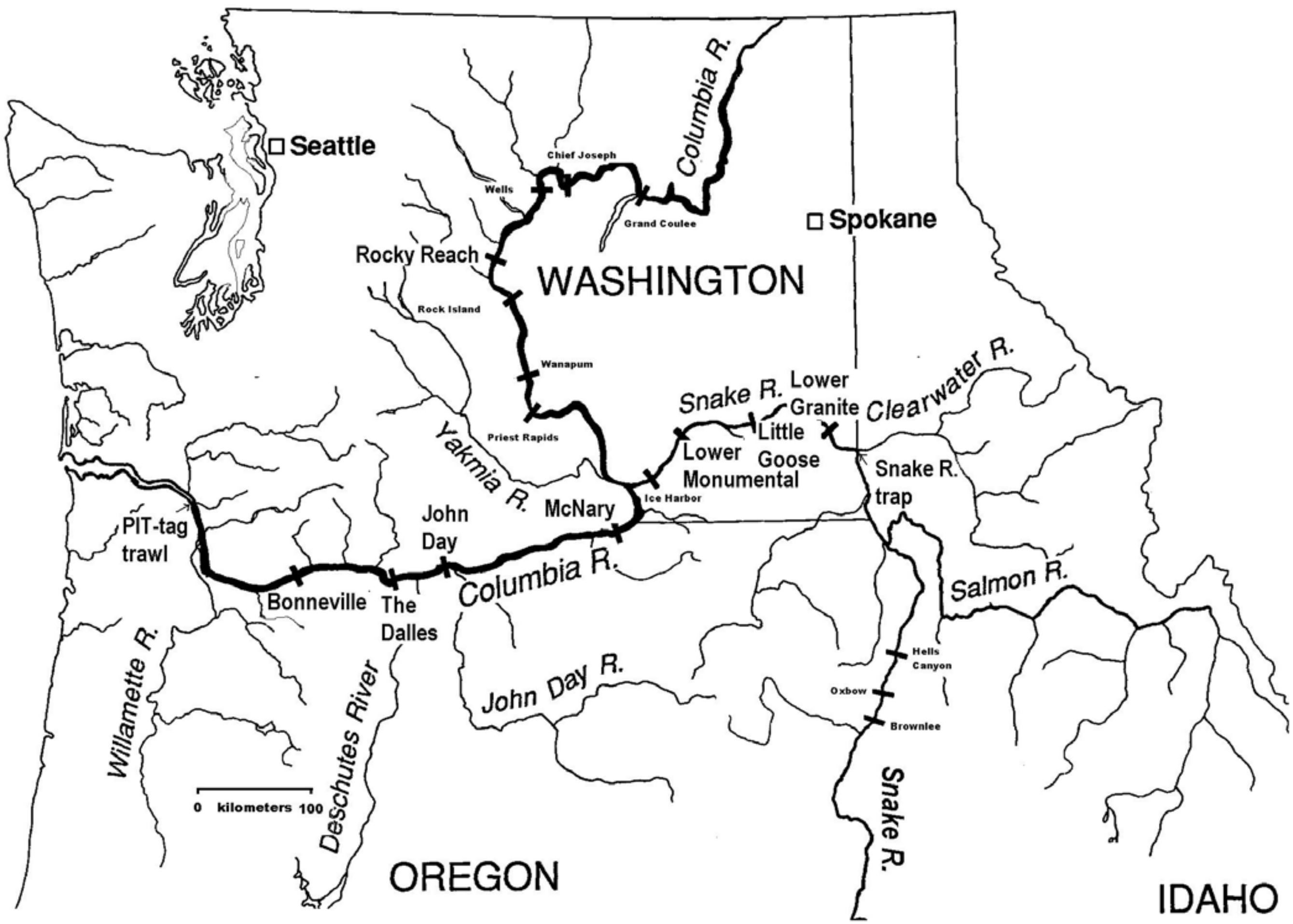


Figure 1. Map of the Columbia River basin showing major dams. PIT-tag detection sites at traps, dams, and the PIT-trawl in larger bold type.

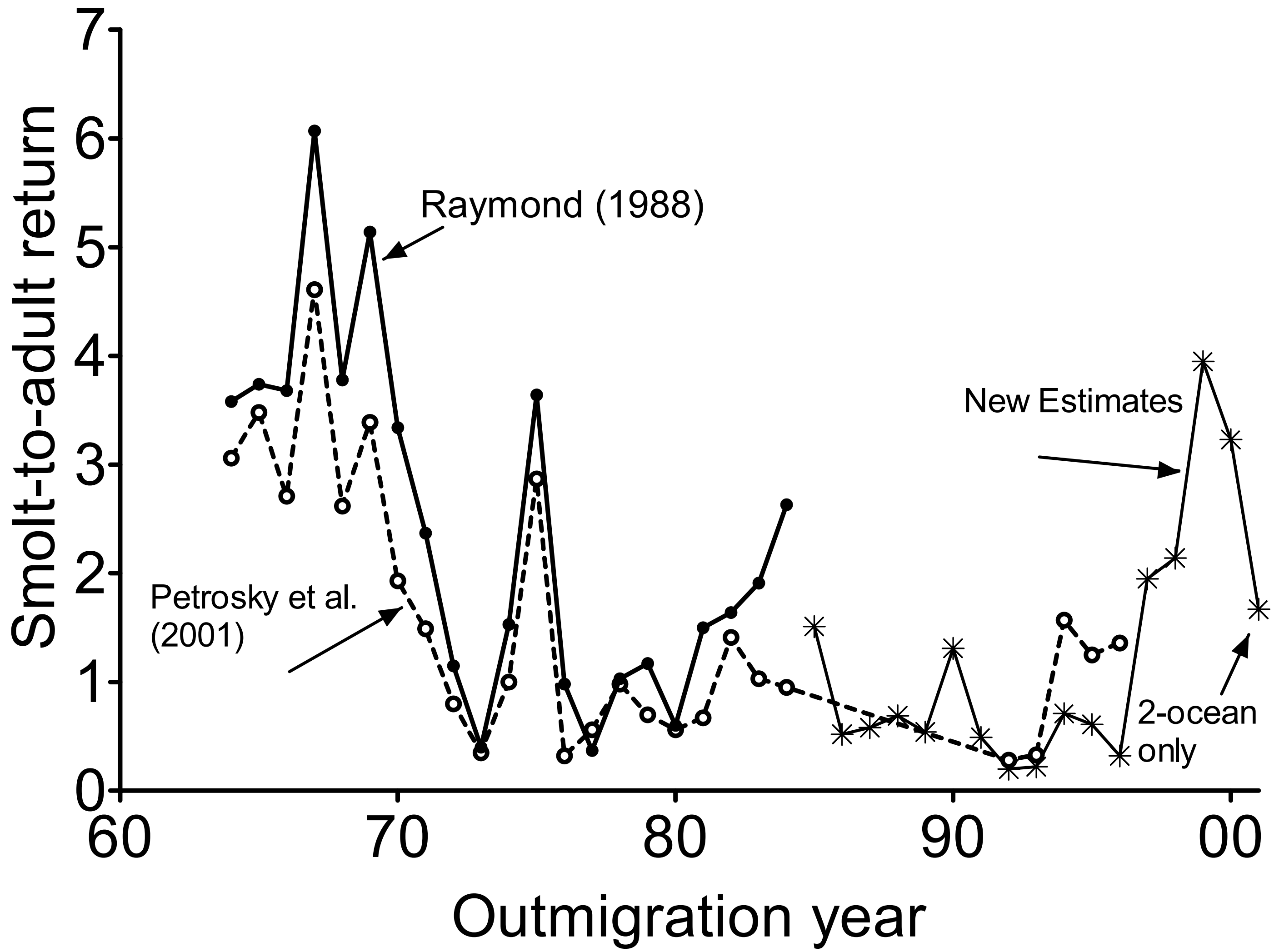


Figure 2. Estimated smolt-to-adult return rates for wild Snake River spring-summer chinook salmon. Initial estimates from 1964 to 1984 from Raymond {, 1988 #262}. Petrosky et al. {, 2001 #49} used Raymond's smolt estimates but a new algorithm to develop alternative SARs for the 1964 to 1984 period. They also estimated SARs for outmigration years 1992-1996.

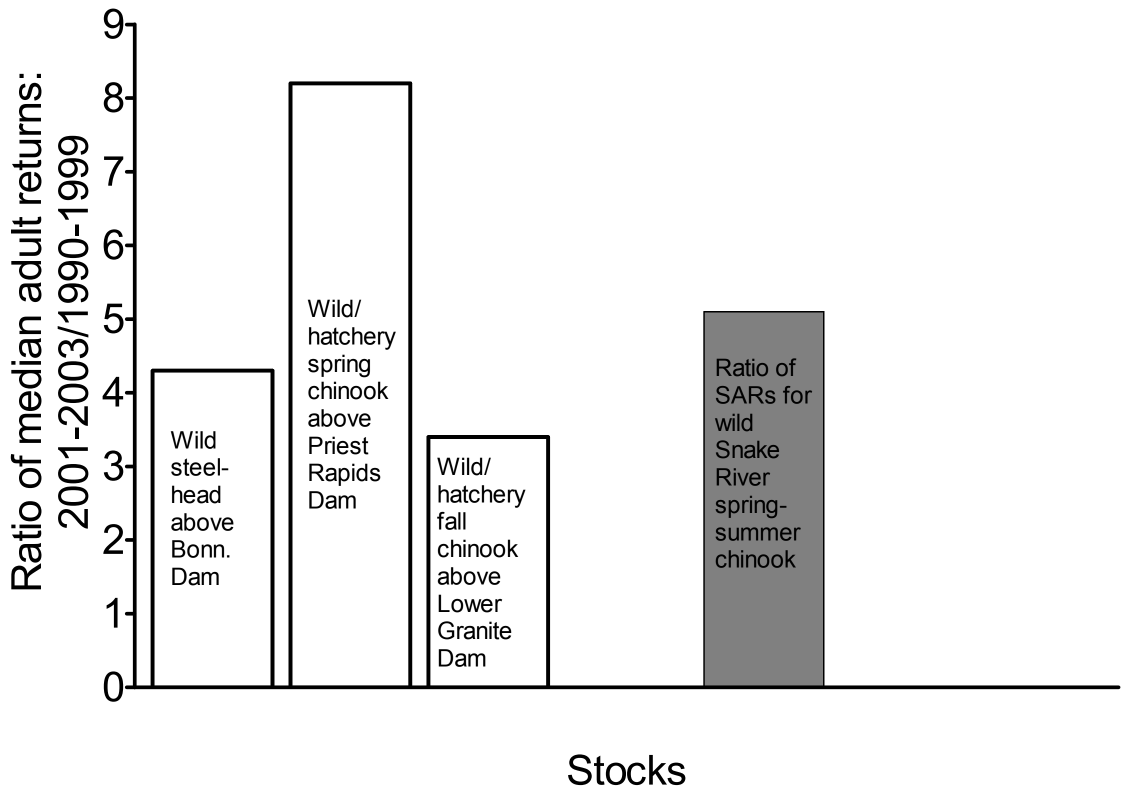


Figure 3. Ratio of the median adult count (2001-2003) of fish (from DART) for wild steelhead at Bonneville Dam and hatchery/wild spring chinook at Priest Rapids Dam divided by the median count at each respective dam for the period 1993-1999 for steelhead and 1991-1999 for chinook. Data for fall chinook salmon from information supplied to the chinook salmon BRT and TAC (see text for details).

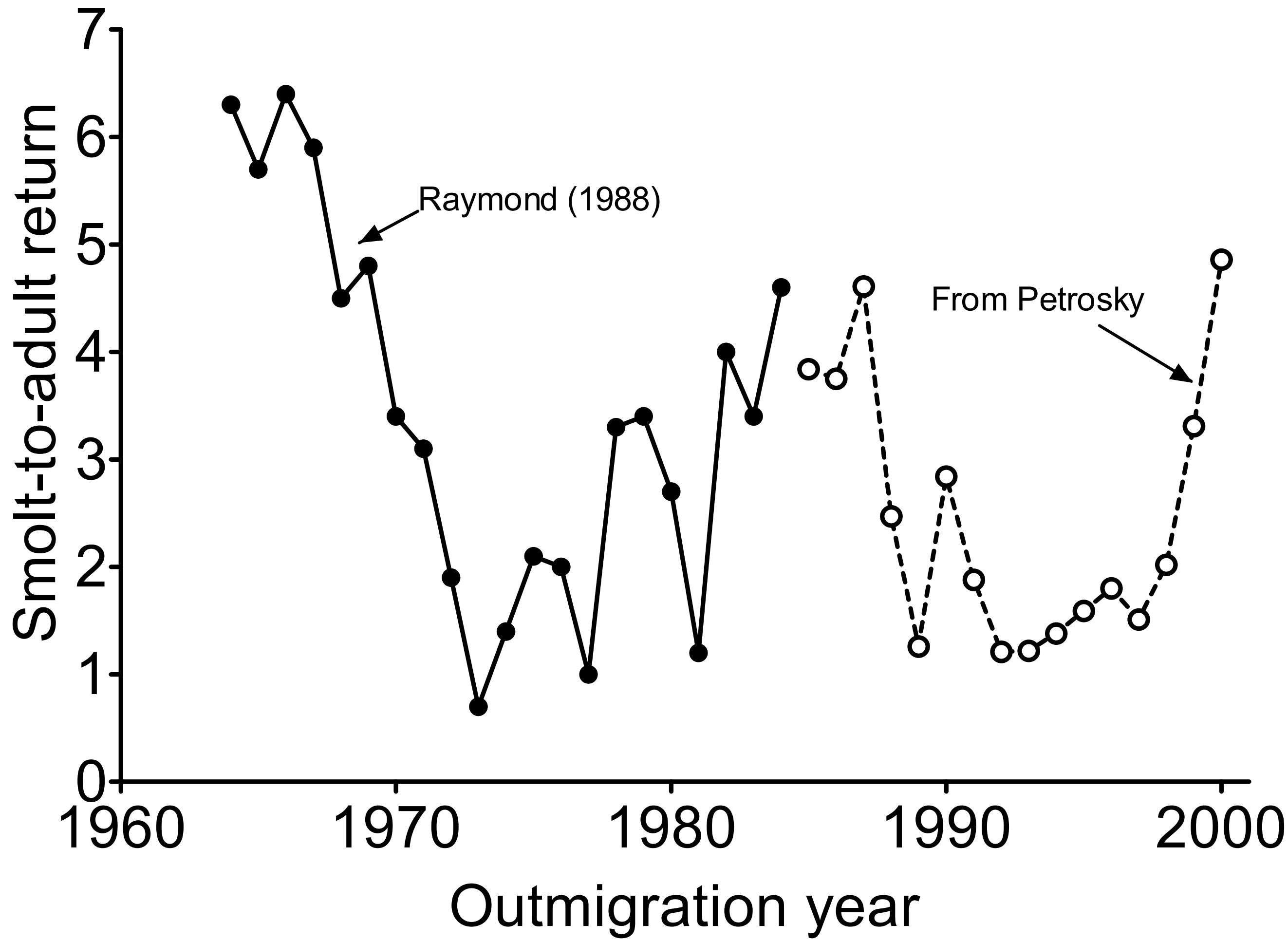


Figure 4. Estimated smolt-to-adult return rates of wild Snake River steelhead. Early data from Raymond {, 1988 #262}. Data 1985 to 2000 (19985 to 1994 from Petrosky submitted to PATH - see {Marmorek, 1998 #336}) and data from 1995 to 2000 unpublished (Charlie Petrosky, IDFG, personal communication).

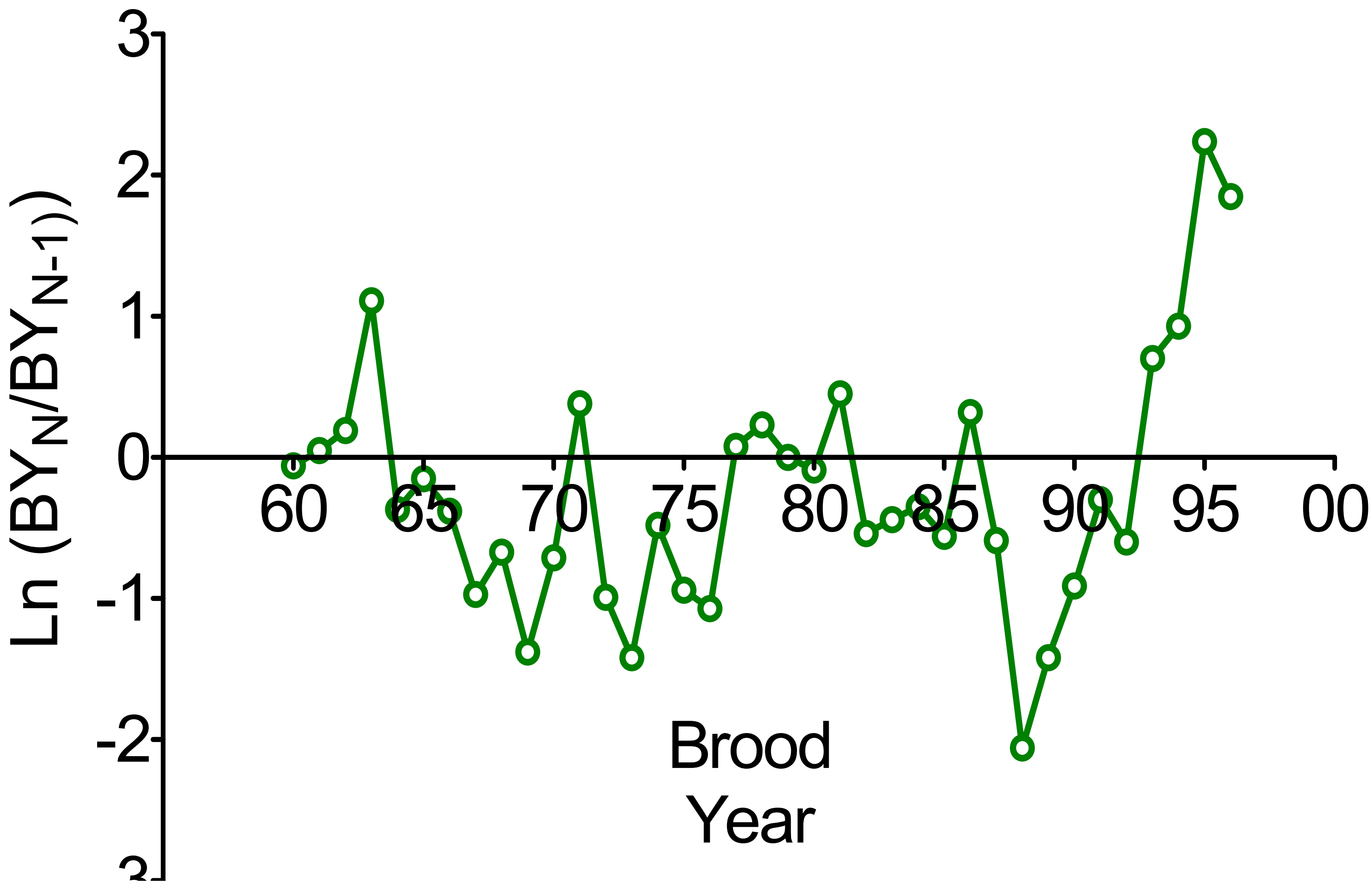


Figure 5. The ln(BY_N = escapement over the upper Snake River dam for the current brood/BY_{N-1} = escapement over the upper Snake River Dam for the brood that produced offspring for current brood) for the composite wild spring-summer chinook salmon population in the Snake River Basin above the upper Snake River Dam (Ice Harbor in 1962, Lower Monumental in 1969, Little Goose in 1970 , and Lower Granite in 1975).

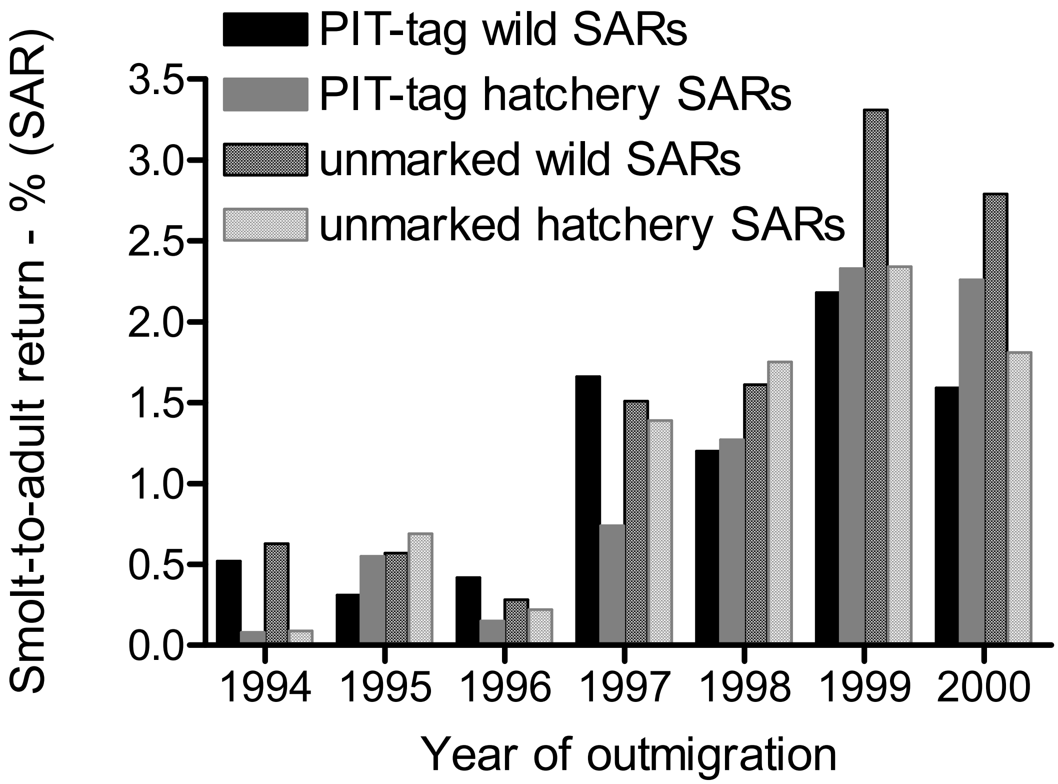


Figure 6. Estimated smolt-to-adult return rates (SARs) for Snake River wild and hatchery spring-summer chinook salmon based on analyses of adult returns from the general untagged population and from SARs for PIT-tagged fish weighted by the estimated migration distribution of the untagged juvenile population. Total returns of PIT-tagged wild fish equaled 26, 60, 16, 40, 211, 720, and 594 from the outmigration years 1994 to 2000, respectively. For the same years, total hatchery adult returns equaled 22, 14, 154, 87, 682, 1690, 3110, and 2878, respectively.

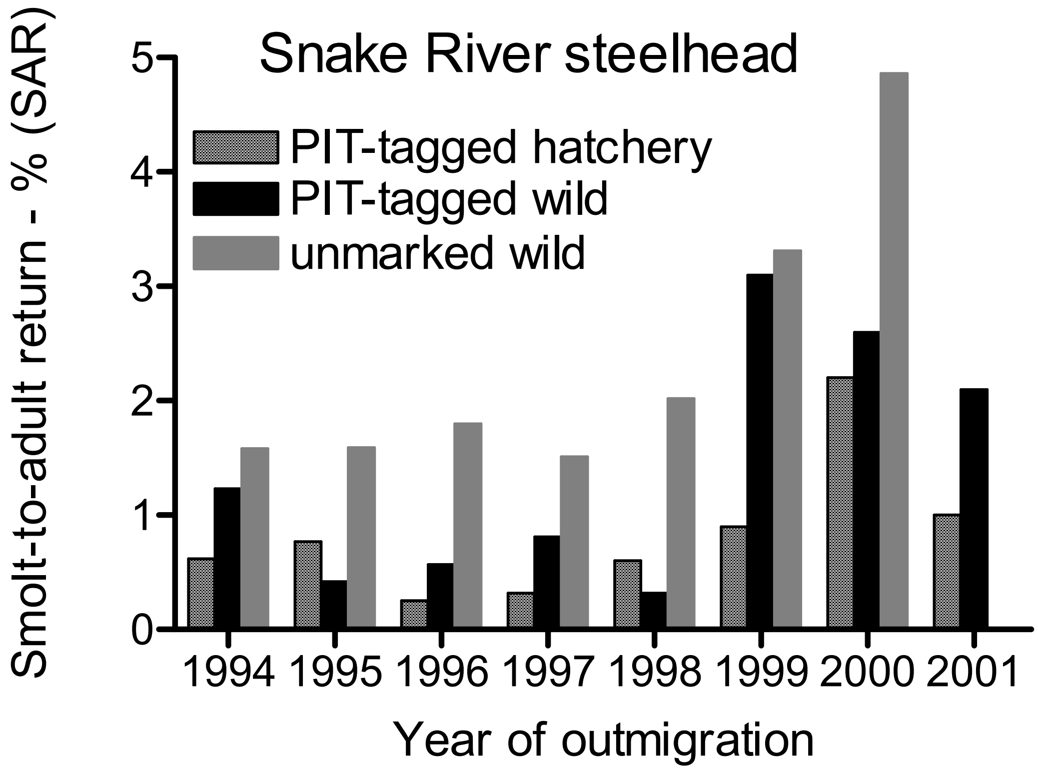


Figure 7. Estimated smolt-to-adult return rates (SARs) for Snake River wild and hatchery steelhead based on analyses of fish PIT-tagged as juveniles or the overall unmarked population (wild only). All analyses based on juveniles and adults at Lower Granite Dam. Total returns of adult PIT-tagged wild fish from the 1994 through 2001 outmigrations equaled 21, 8, 15, 13, 25, 101, 283, 11, respectively. Total adult returns for hatchery fish from the same outmigration years equalled 51, 104, 69, 49, 76, 186, 267, and 9, respectively.

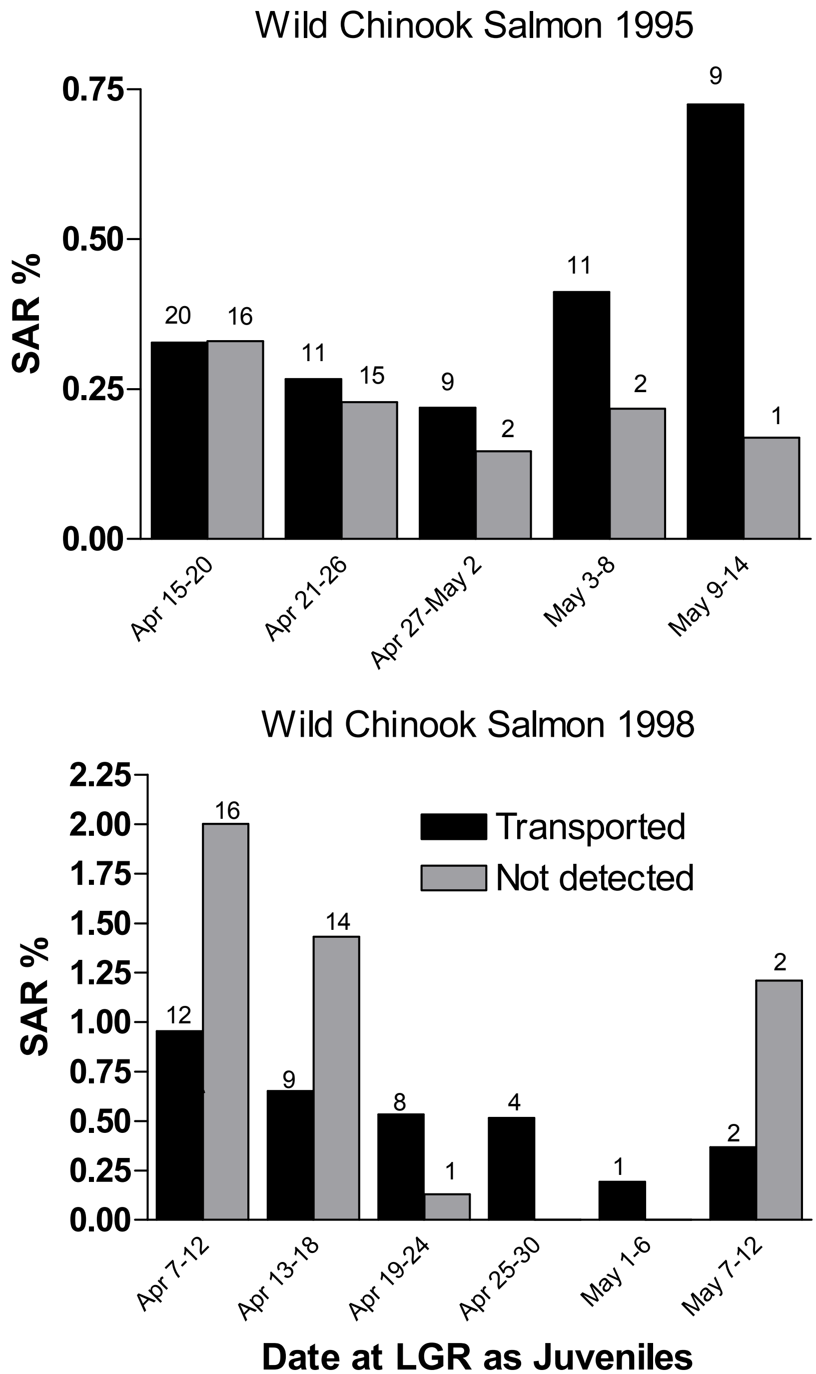


Figure 8. Temporal change in SARs of wild Snake River spring-summer chinook salmon PIT-tagged at Lower Granite Dam, 1995 and 1998. No significant differences in return rates detected between pairs of treatment groups. Numbers above the bars indicate total adult returns for each group.

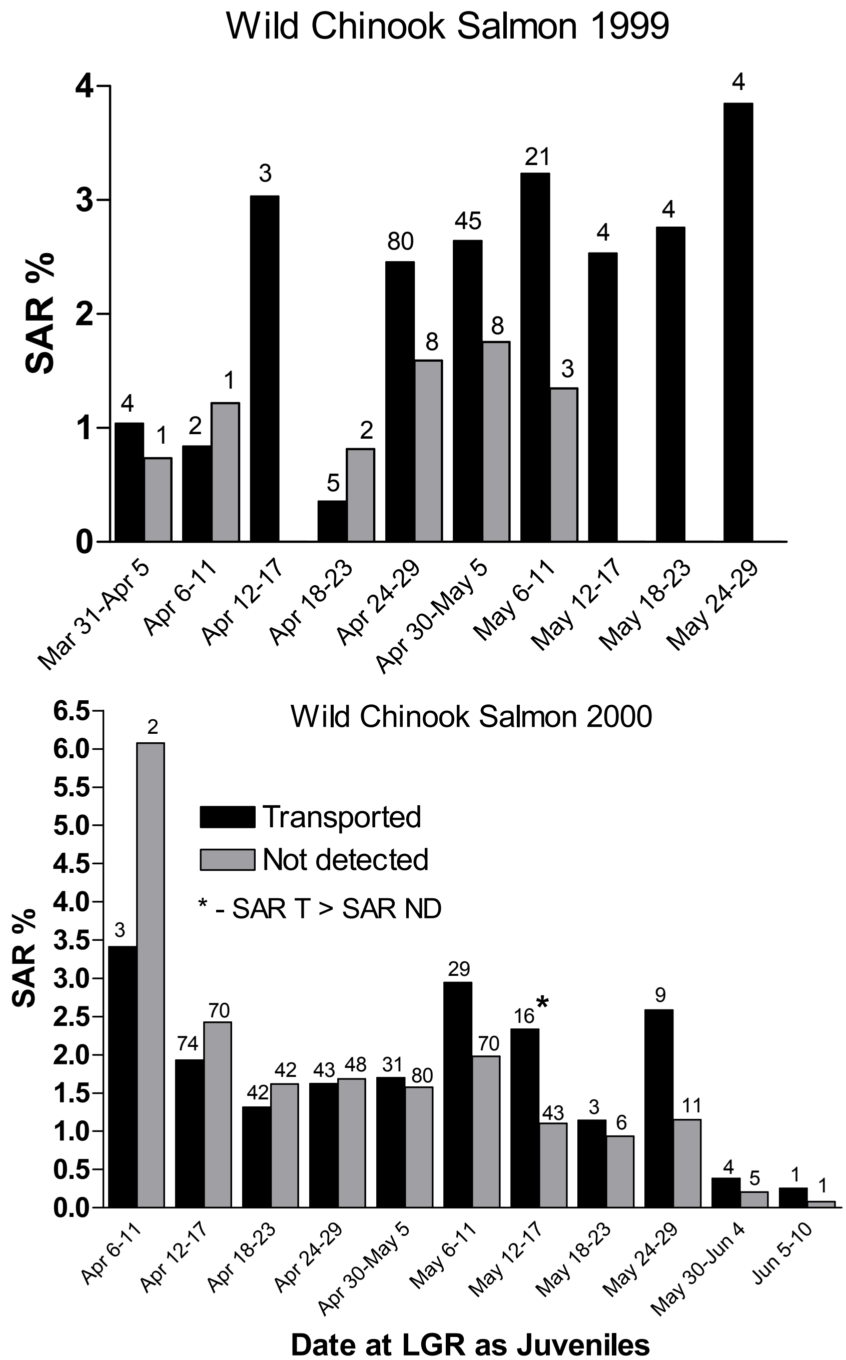


Figure 9. Temporal change in SARs of wild Snake River spring-summer chinook salmon PIT-tagged at Lower Granite Dam, 1999 and 2000. In 2000, in one treatment pair, transported fish returned at significantly higher rates. Numbers above the bars indicate the total adult returns for each group.

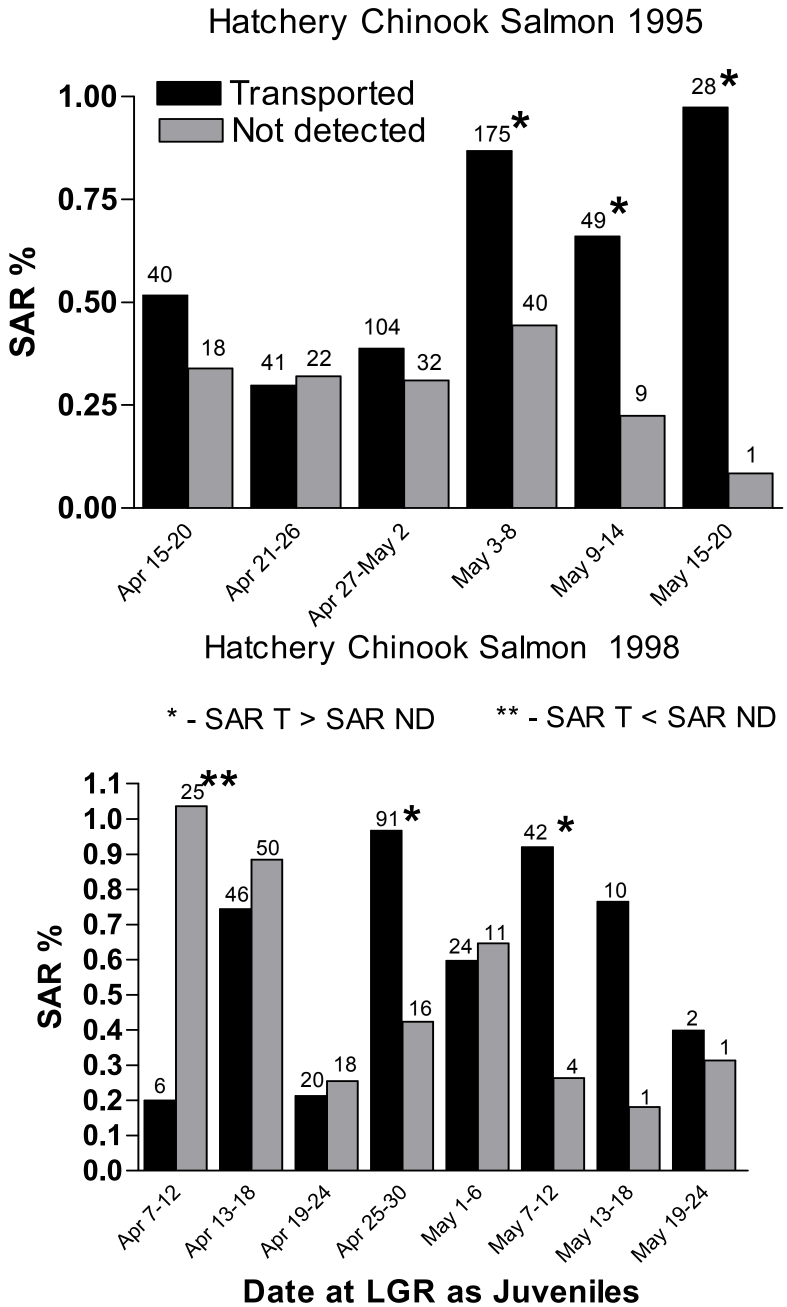


Figure 10. Temporal change in SARs of hatchery Snake River spring-summer chinook salmon PIT-tagged at Lower Granite Dam, 1995 and 1998. Significantly higher (*) return rates of transported fish occurred for several treatment pairs in both years. A significantly higher (**) return rate of non-detected fish occurred for one treatment pair in 1998.

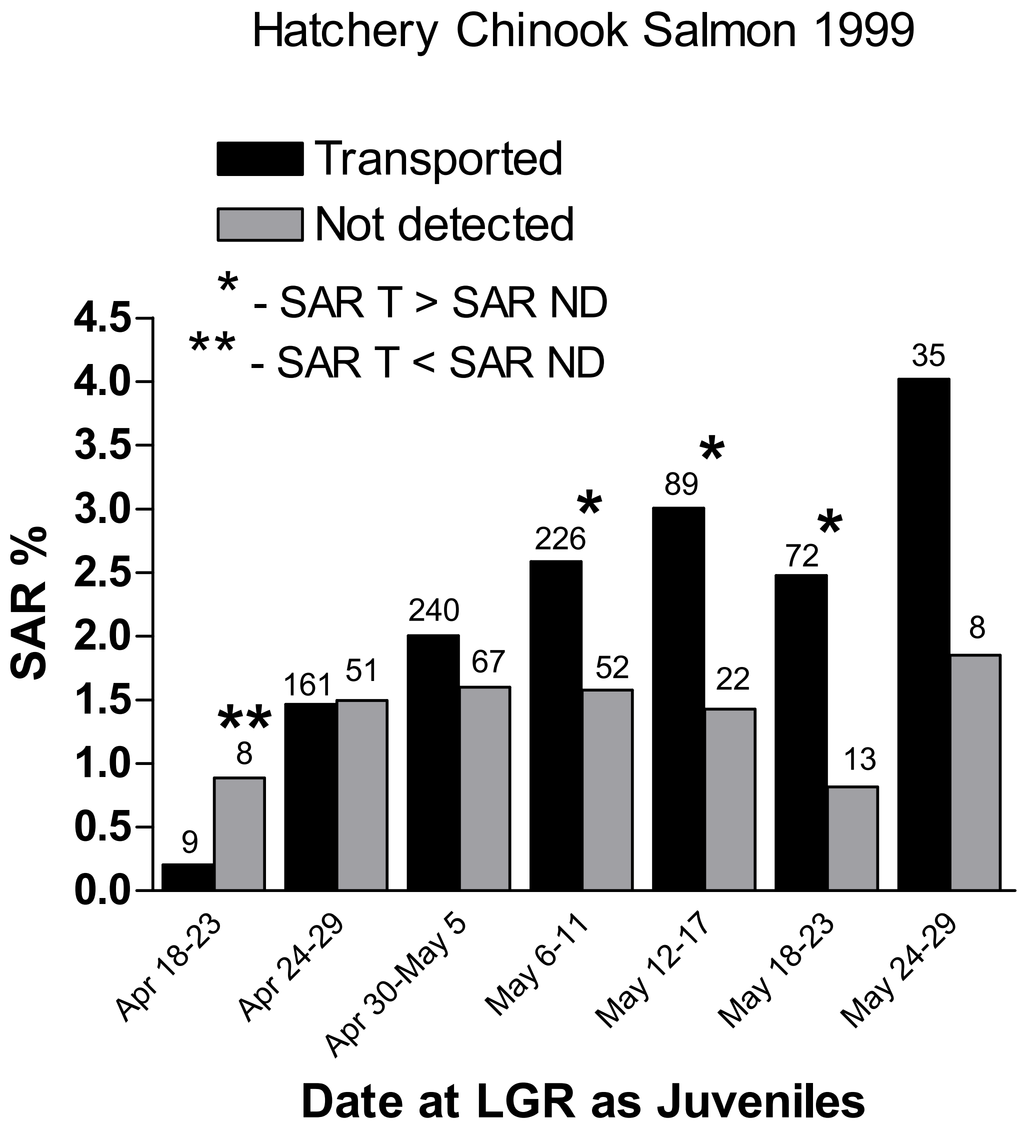


Figure 11. Temporal change in SARs of hatchery Snake River spring-summer chinook salmon PIT-tagged at Lower Granite Dam, 1999. Significantly higher (*) return rates occurred for transported fish in several treatment pairs. A significantly higher return rate for non-detected fish occurred in one treatment pair.

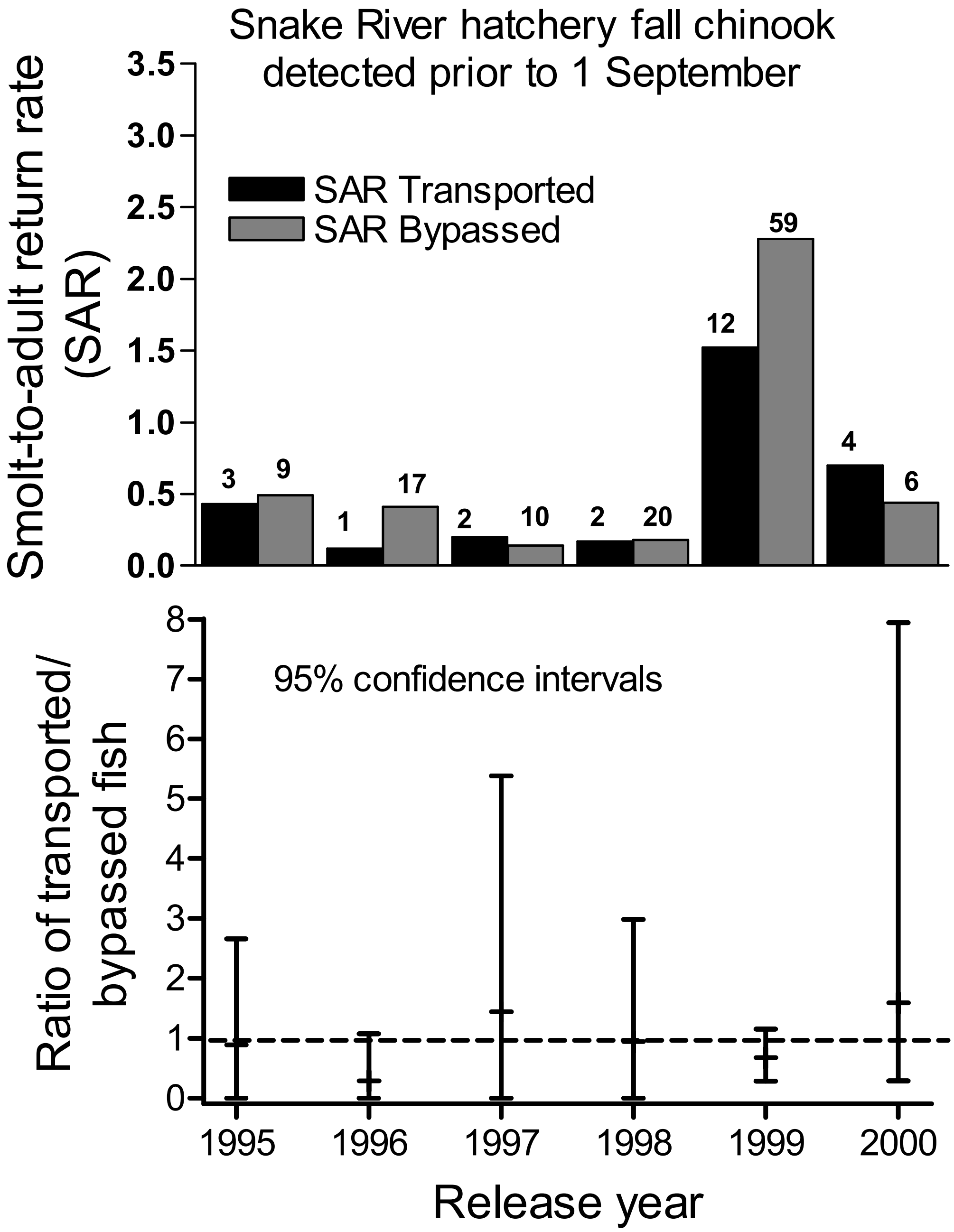


Figure 12. Smolt-to-adult return rates of PIT-tagged hatchery Snake River fall chinook salmon released above Lower Granite Dam and bypassed or transported from Lower Granite, Little Goose, Lower Monumental, or McNary Dam (not adjusted to Lower Granite Dam equivalents) prior to 1 September, with ratios of transported/bypassed fish and 95% confidence bounds.

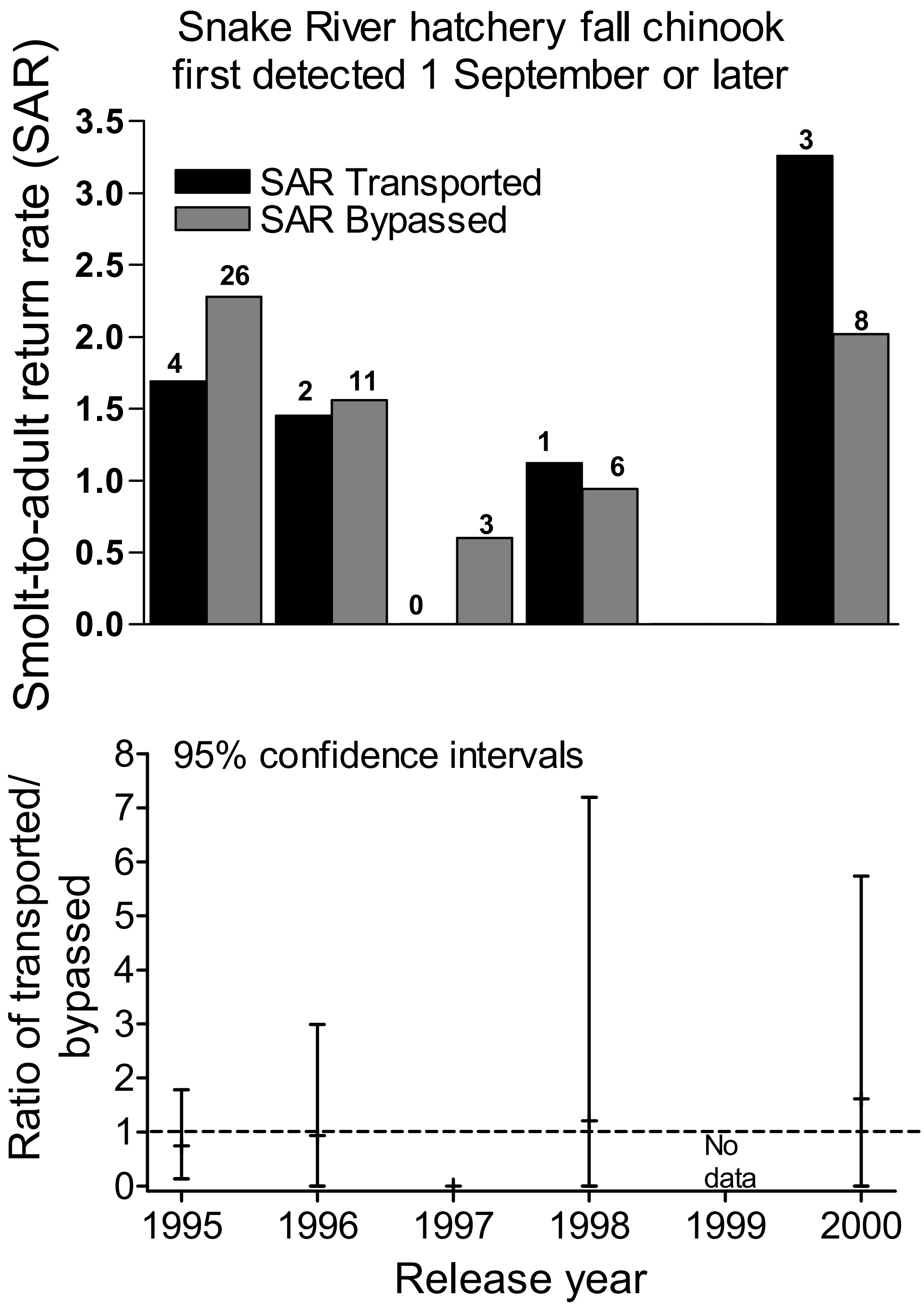


Figure 13. Smolt-to-adult return rates of PIT-tagged hatchery Snake River fall chinook salmon released above Lower Granite Dam and bypassed or transported from Lower Granite, Little Goose, Lower Monumental, or McNary Dam (not adjusted to Lower Granite Dam equivalents) on 1 September or later, with rates fo transported/bypassed fish and 95% confidence bounds.

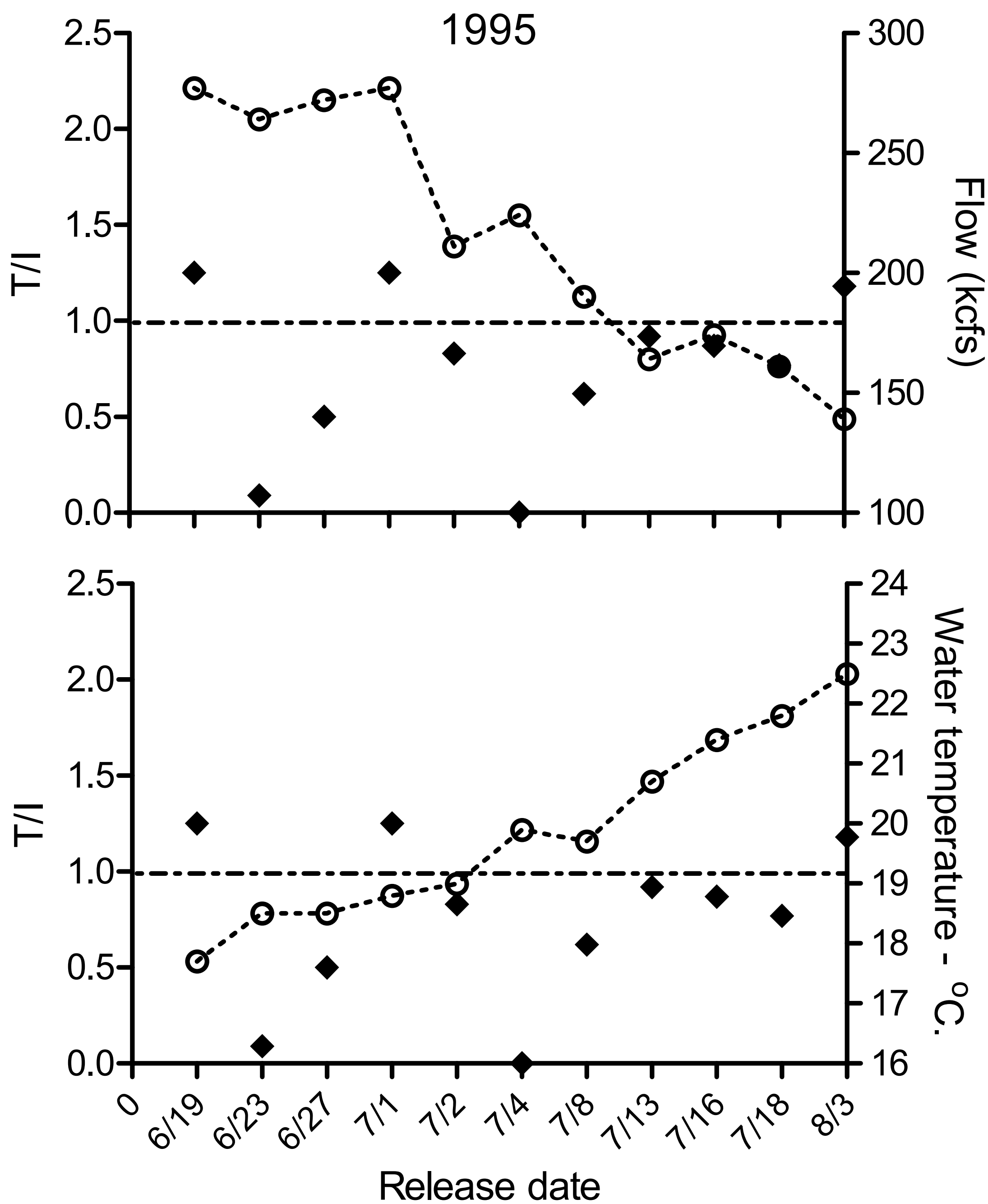


Figure 14. Relative recovery rates of coded-wired-tagged (CWT) adult summer/fall chinook salmon recovered from fisheries or at hatcheries from subyearling fish tagged as juveniles in 1995 at McNary Dam and either transported (T) to below Bonneville Dam or released into the tailrace of McNary Dam (I = in-river).

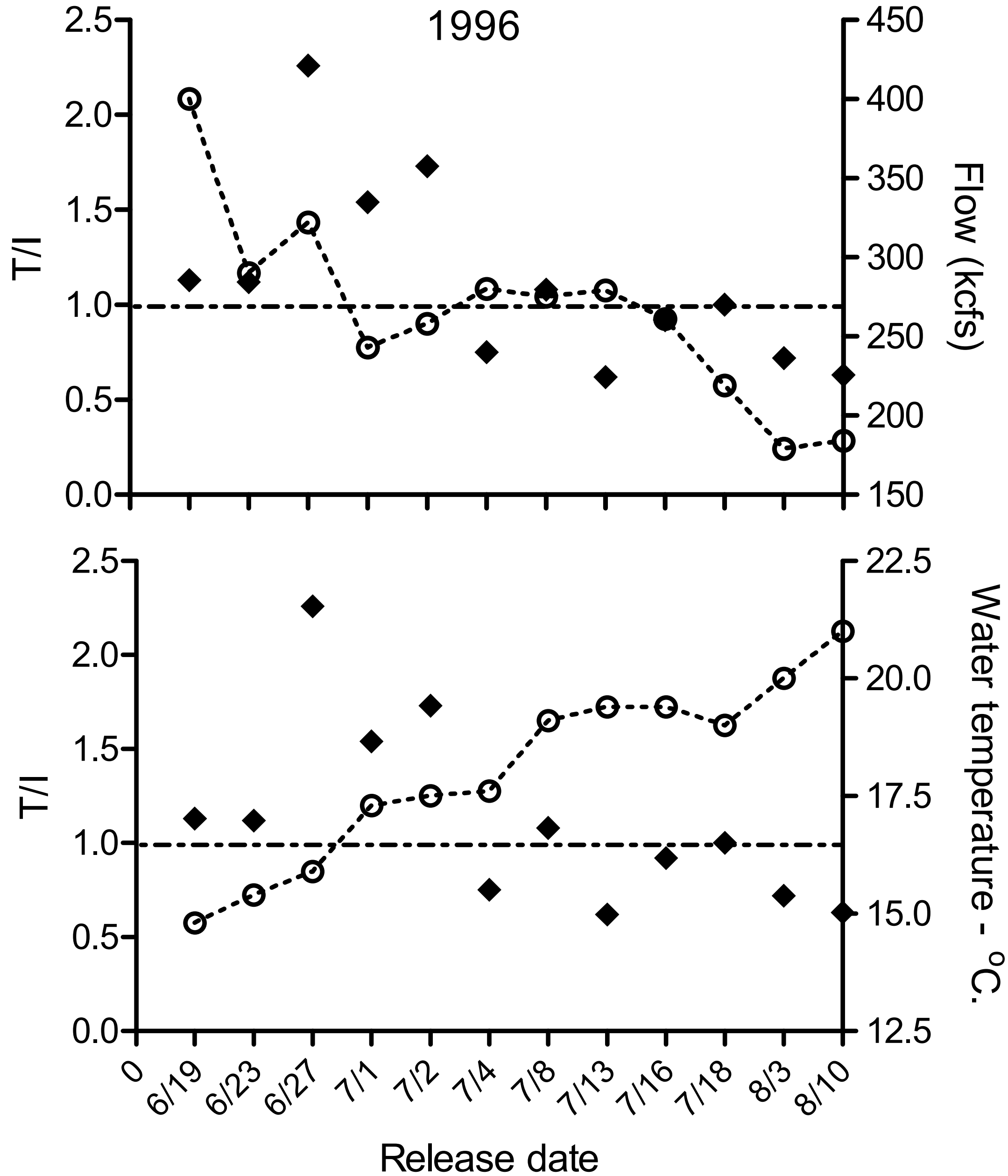


Figure 15. Relative recovery rates of coded-wire-tagged (CWT) adult summer/fall chinook salmon recovered in fisheries or at hatcheries from subyearling fish tagged as juveniles at McNary Dam in 1996 and either transported (T) to below Bonneville Dam or released into the tailrace of McNary Dam (I = in-river).

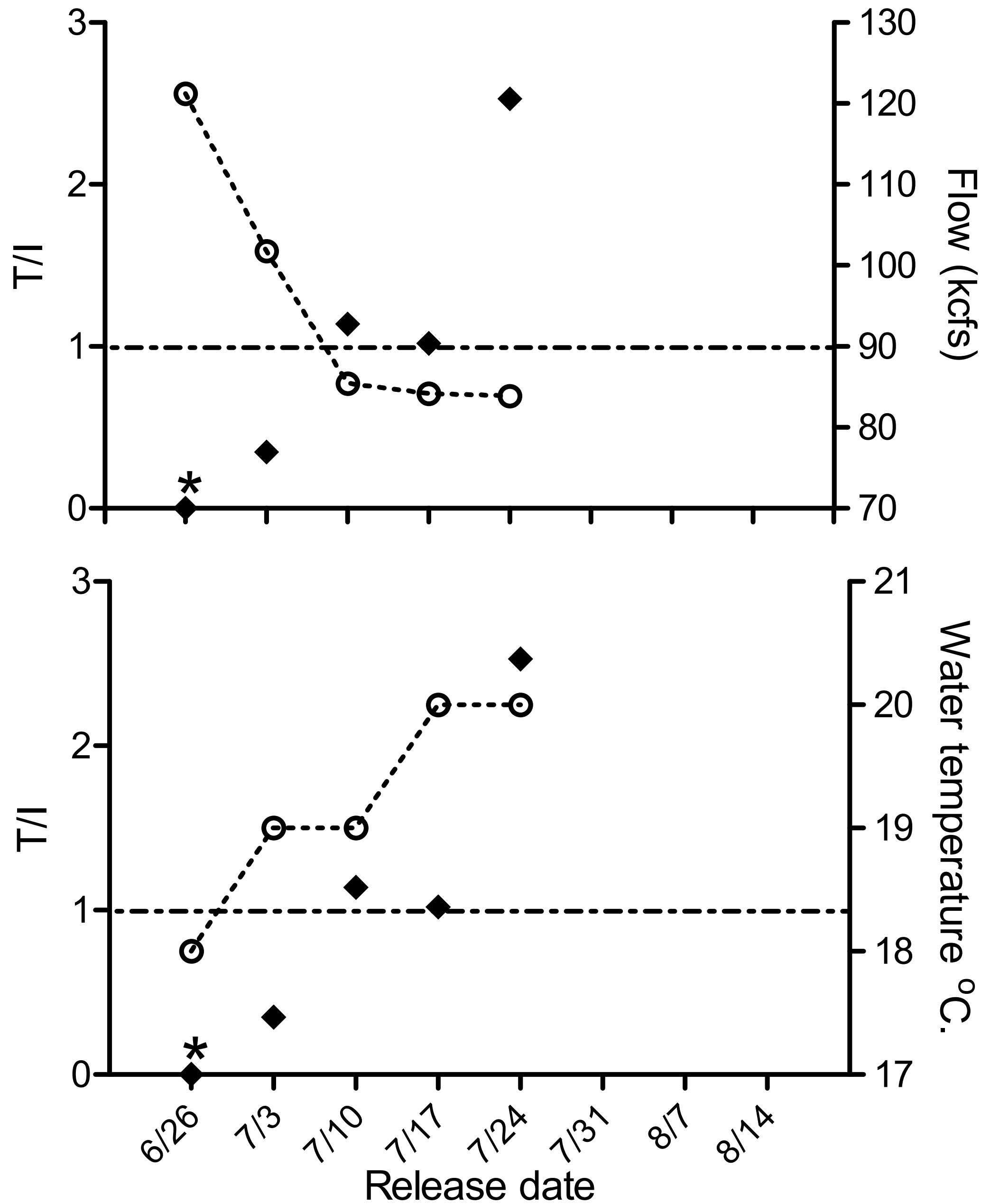


Figure 16. PRELIMINARY T/I ratios based on SARs for combined weekly releases of transported and in-river subyearling chinook salmon PIT tagged and released at McNary Dam in 2001, plotted with weekly average water temperature and flow. (Only 62 total 1-ocean and 2-ocean fish returned to data.) * indicates no transported fish returned.

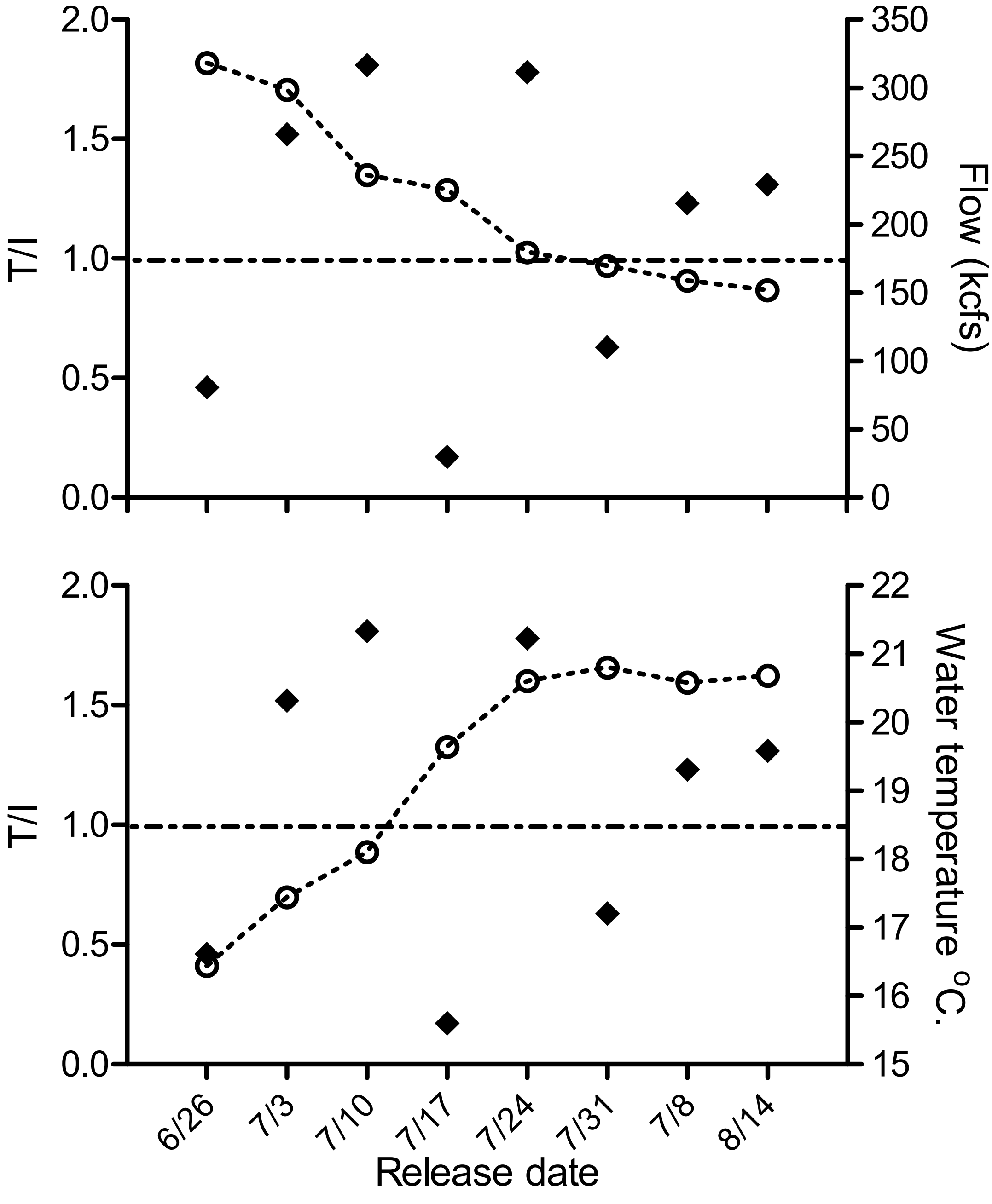


Figure 17. PRELIMINARY T/I ratios based on SARs for combined weekly releases of transported and in-river subyearling chinook salmon PIT-tagged and released at McNary Dam in 2002, plotted with the weekly average water temperature and flow. (Only 143 total 1-ocean fish have returned to date.)

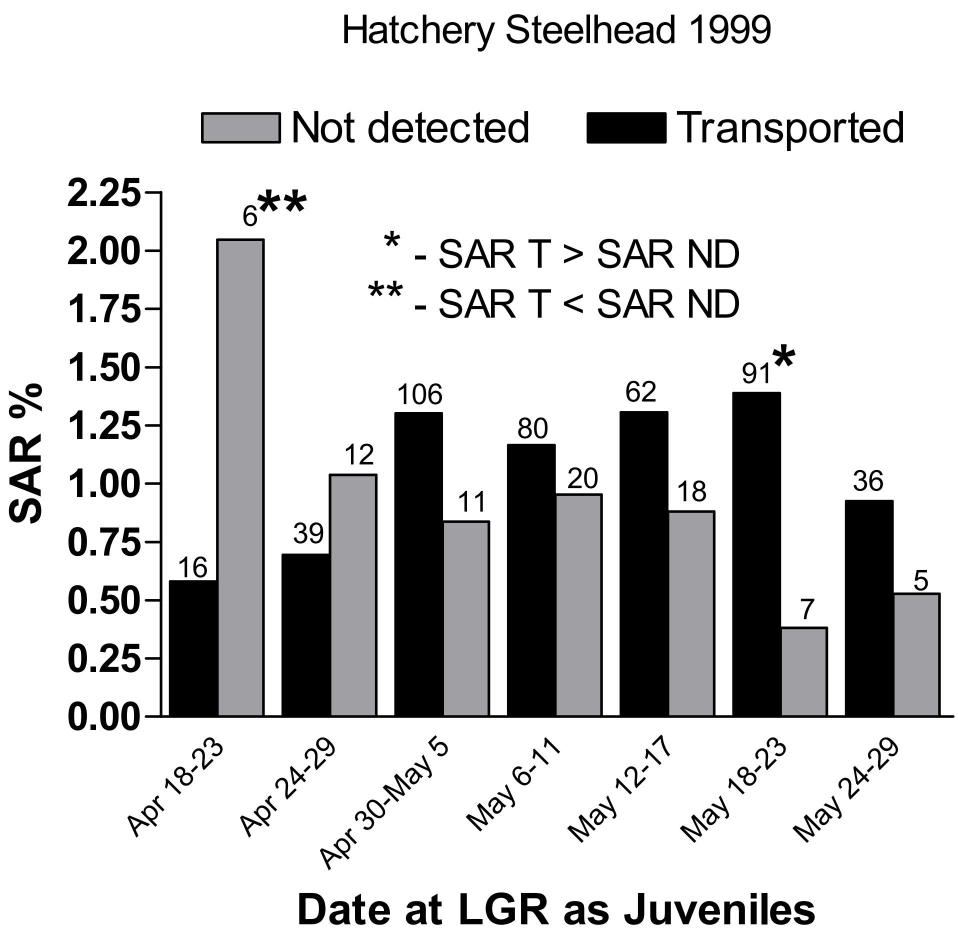


Figure 18. Temporal change in SARs of hatchery Snake River steelhead PIT-tagged at Lower Granite Dam. In one treatment pair significantly more non-detected fish returned and in one pair significantly more transported fish. Numbers above bars indicate total adult returns for each group.

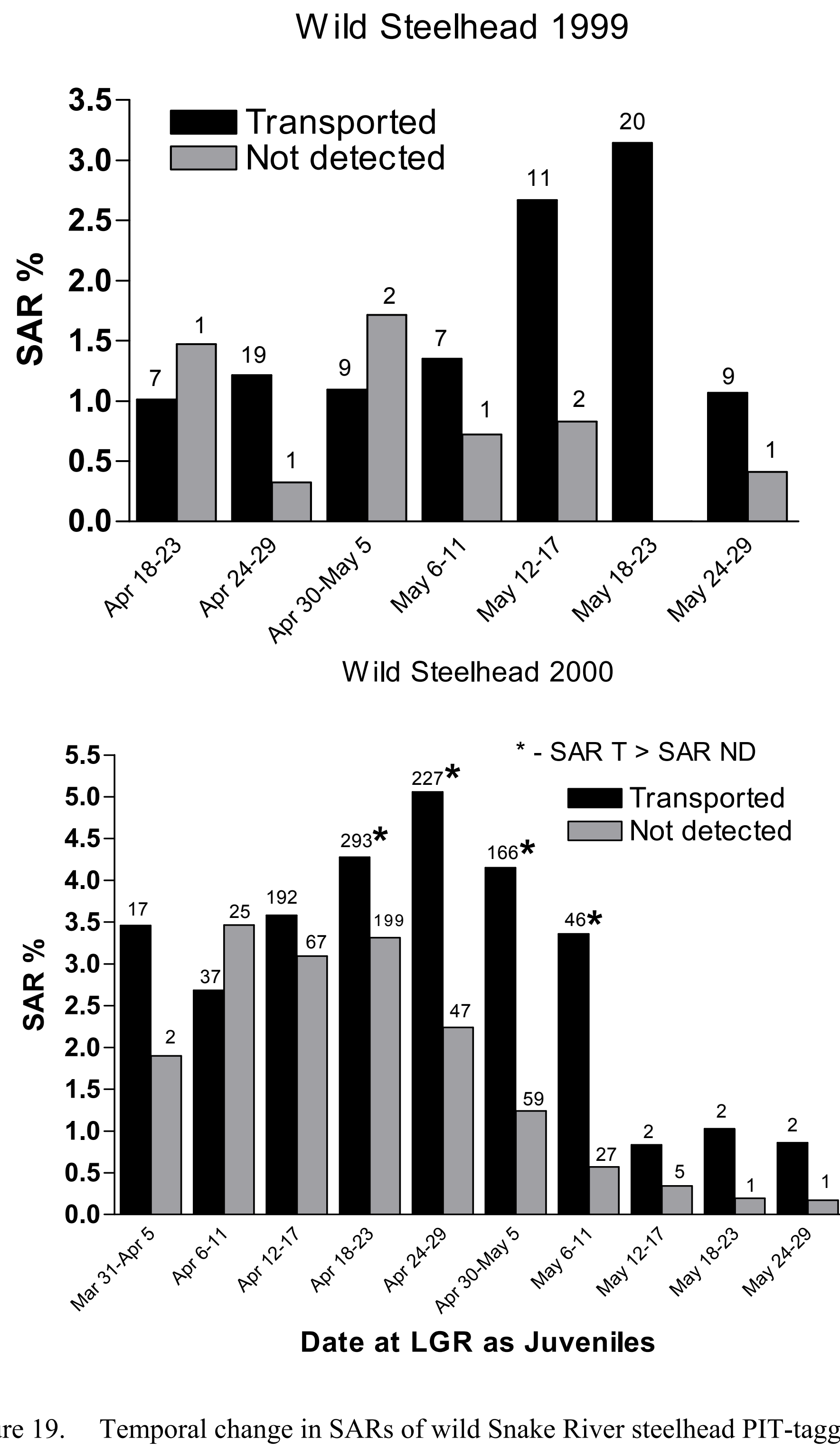


Figure 19. Temporal change in SARs of wild Snake River steelhead PIT-tagged at Lower Granite Dam, 1999 and 2000. During four treatment pairs, significantly more transported fish returned than not detected fish. Number above bars indicate total adult returns for each group.

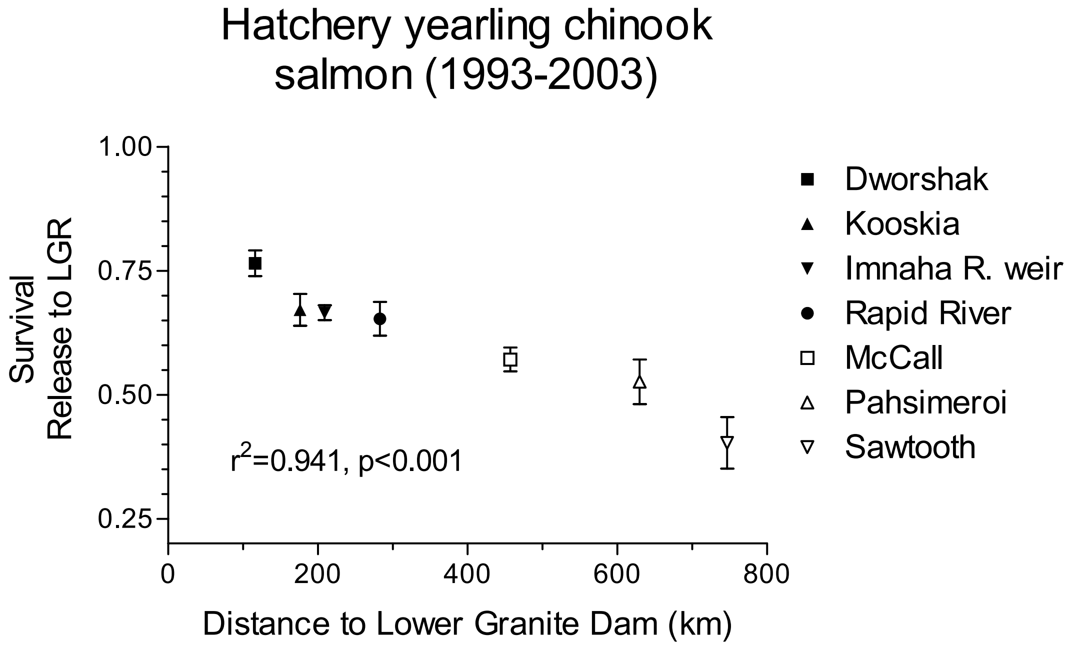


Figure 20. Estimated survival with standard errors from release at Snake River Basin hatcheries to Lower Granite Dam tailrace, 1993-2003 vs distance (km) to Lower Granite Dam. The correlation between survival and migration distance is also shown.

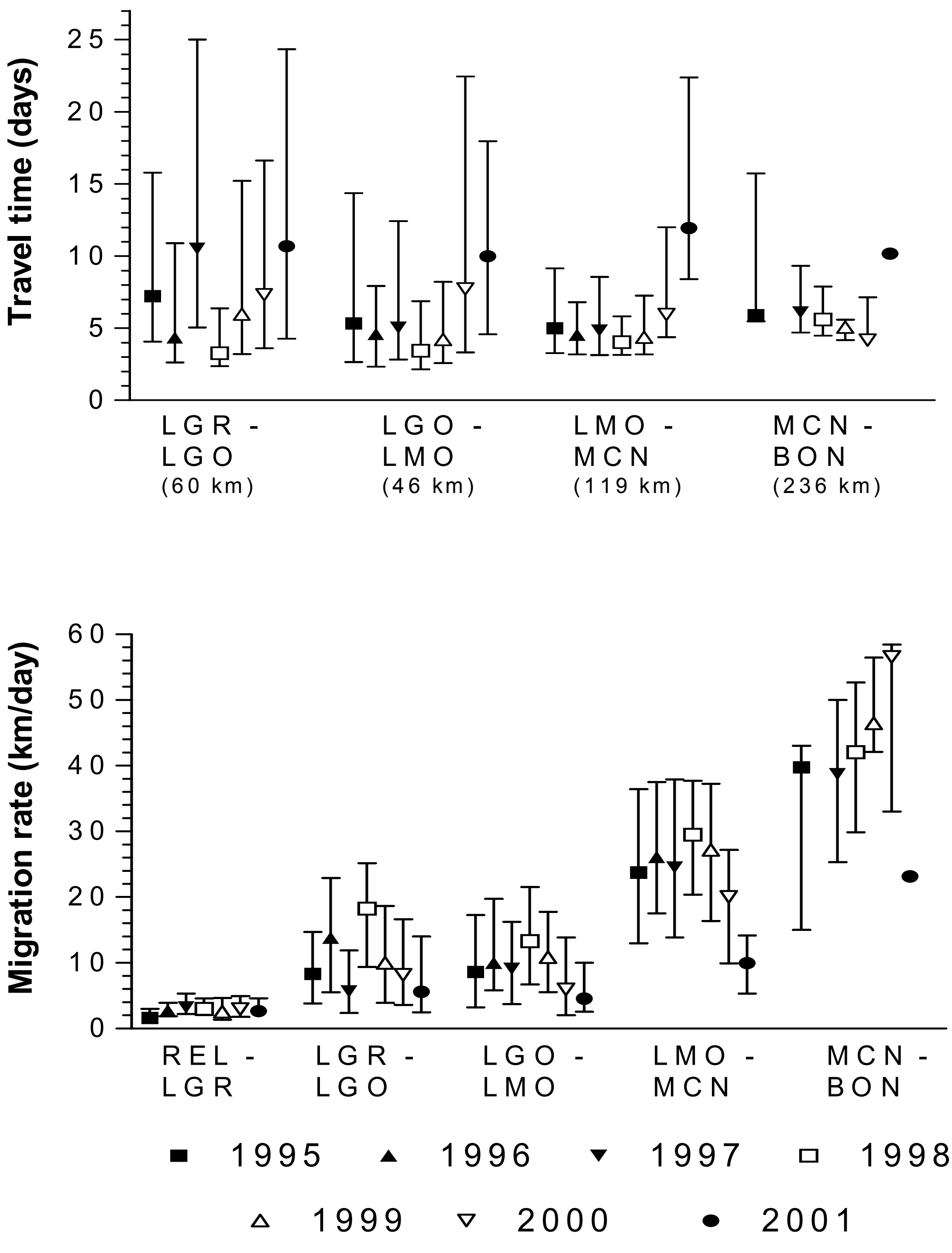


Figure 21. Median travel times and migration rates (with 20th and 80th percentiles) for PIT-tagged hatchery fall chinook salmon, 1995-2001. Rel, release site in the Snake River; LGR, Lower Granite Dam; LGO, Little Goose Dam; LMO, Lower Monumental Dam; MCN, McNary Dam; and BON, Bonneville Dam. The lengths of the reaches are given in parentheses in the upper panel.

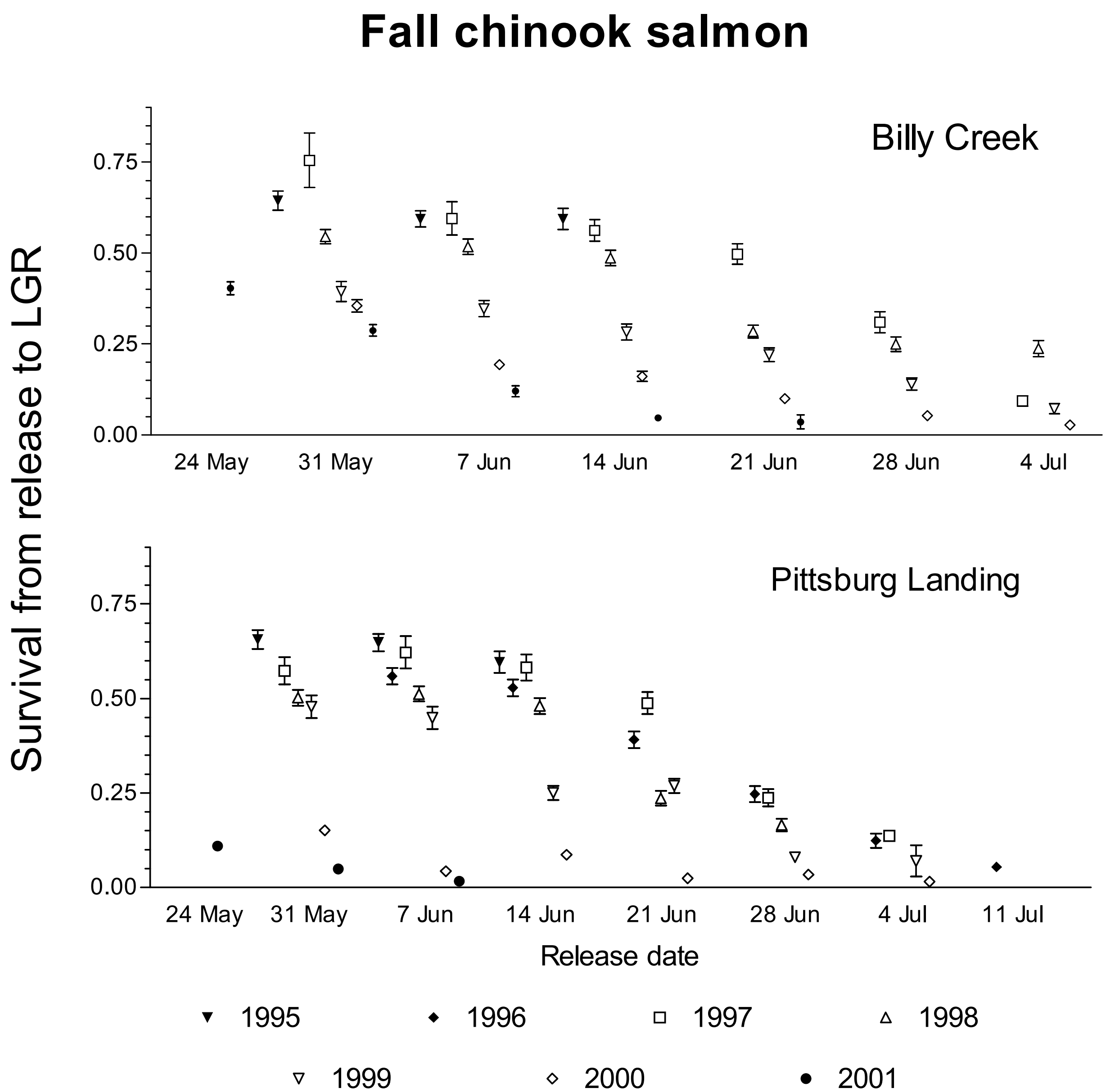


Figure 22. Estimated survival probabilities (with standard errors) from point of release in the Snake River (Billy Creek or Pittsburg Landing) to the tailrace of Lower Granite Dam for PIT-tagged hatchery subyearling fall chinook salmon, 1995-2001.

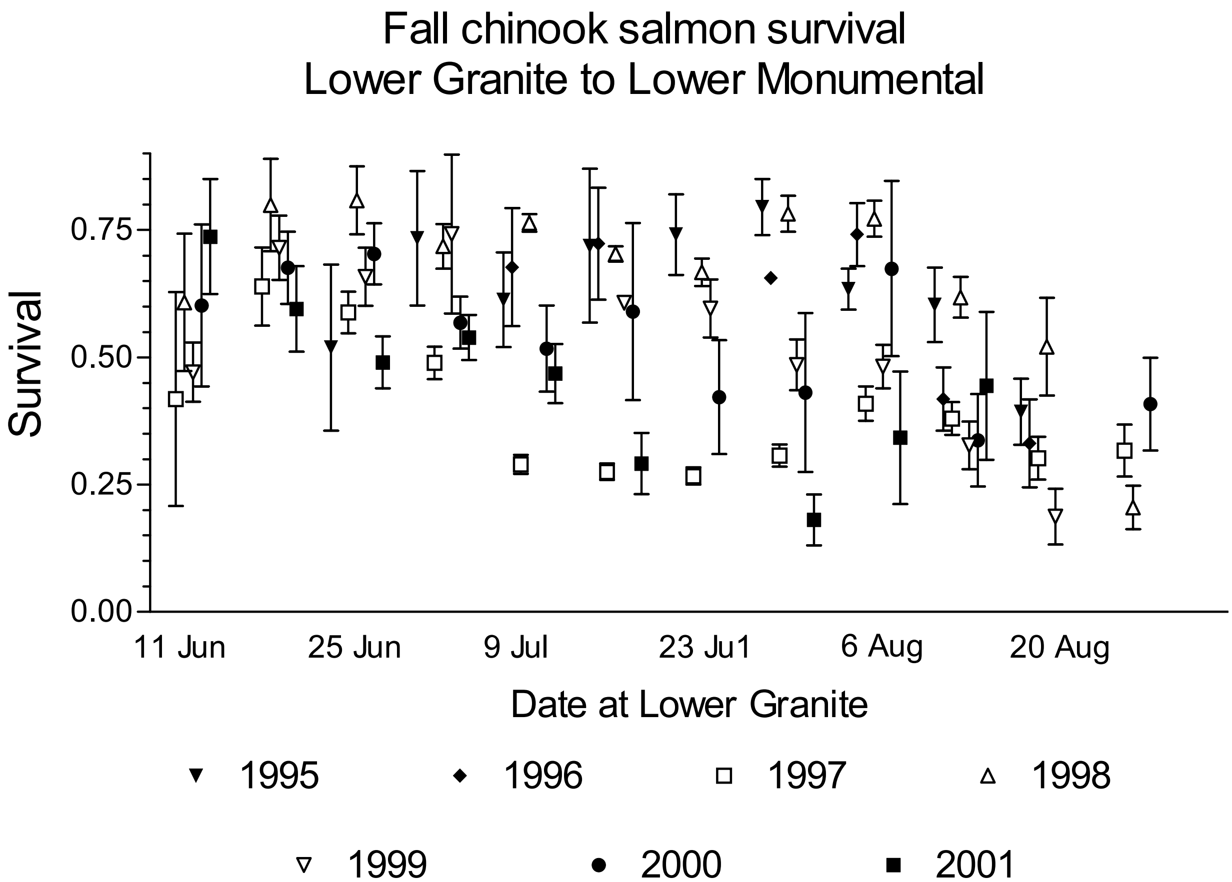


Figure 23. Estimated survival probabilities (with standard errors) to the tailrace of Lower Monumental Dam for PIT-tagged hatchery subyearling fall chinook salmon leaving Lower Granite Dam, by week, 1995-2001.

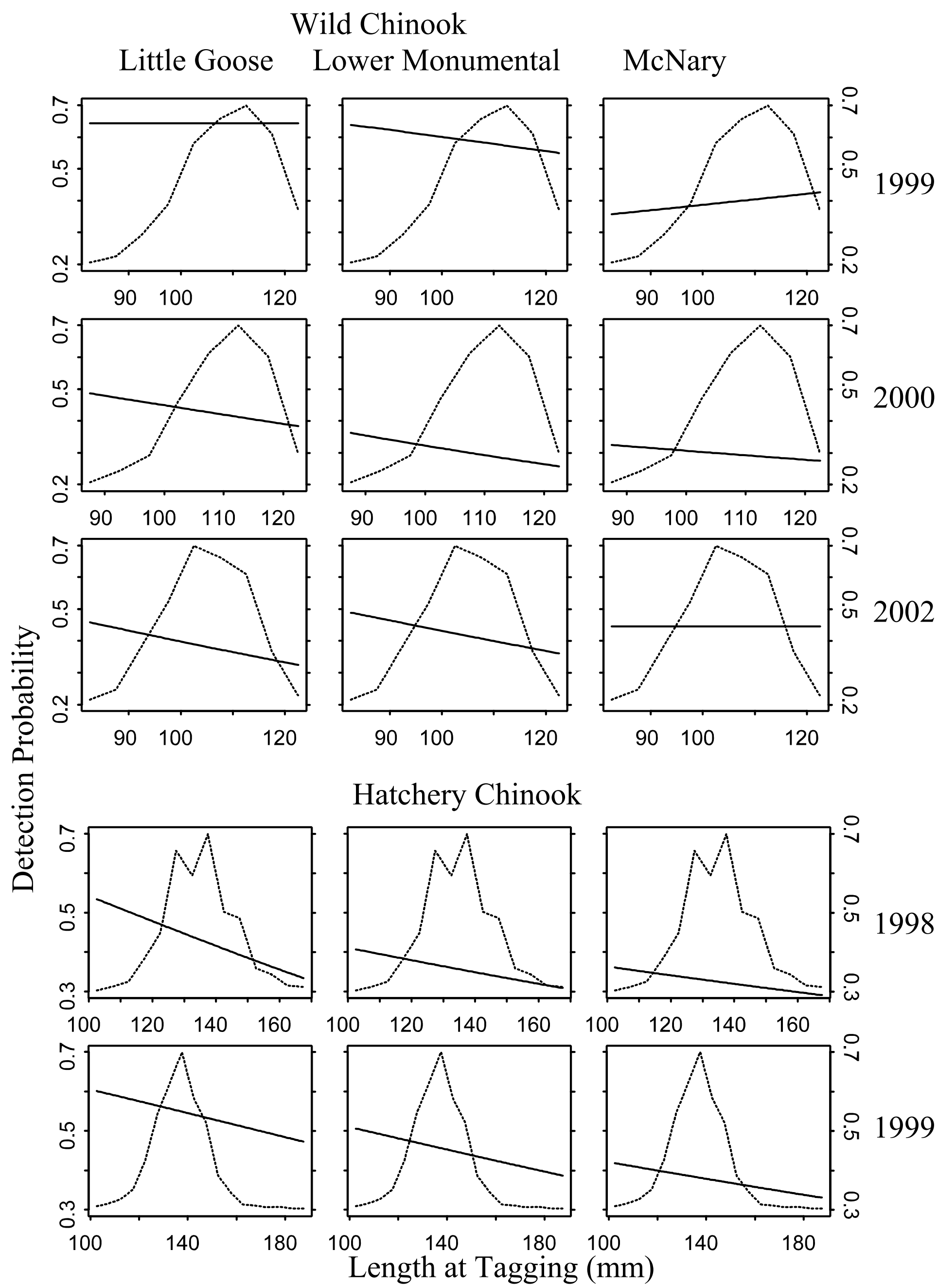


Figure 24. Relationships between detection (solid line) probability and fish length (mm) for Snake River spring/summer chinook salmon released at Lower Granite Dam. The dotted line is the scaled distribution of lengths in 5 mm increments.

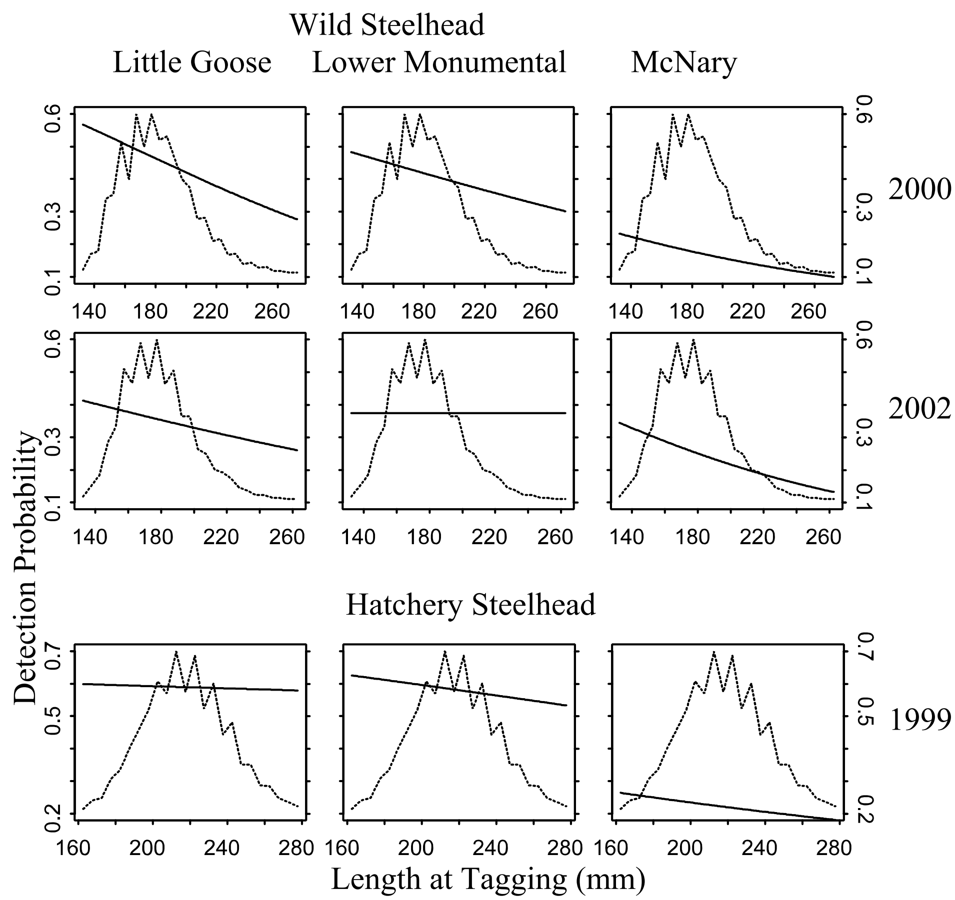


Figure 25. Relationships between detection (solid line) probability and fish length (mm) for Snake River steelhead released at Lower Granite Dam. The dotted line is the scaled distribution of lengths in 5 mm increments.

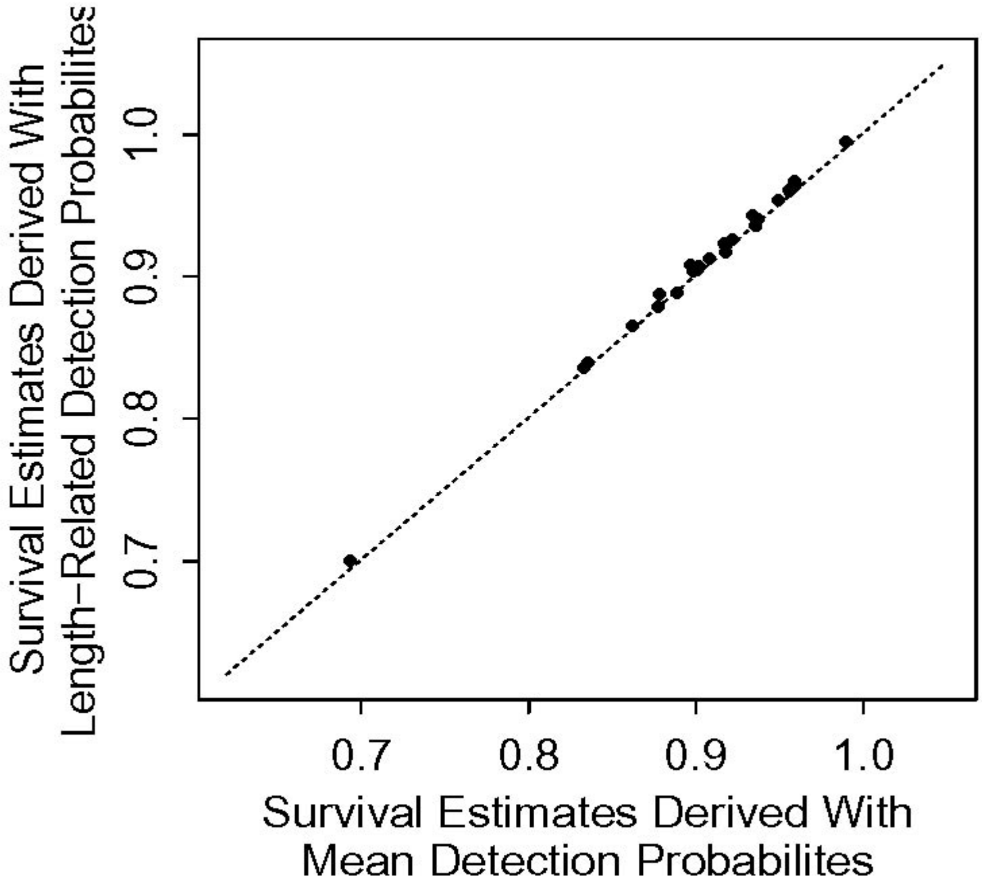


Figure 26. Comparison of survival estimates derived assuming mean detection probabilities (Cormack-Jolly-Seber method) and those using length-related detection probabilities. Wild and hatchery spring/summer chinook salmon and steelhead were tagged and released at Lower Granite Dam (1998-2002), and survival was estimated from Lower Granite to Little Goose Dam, Little Goose to Lower Monumental Dam, and Lower Monumental to McNary Dam. The dashed line is the one-to-one line.

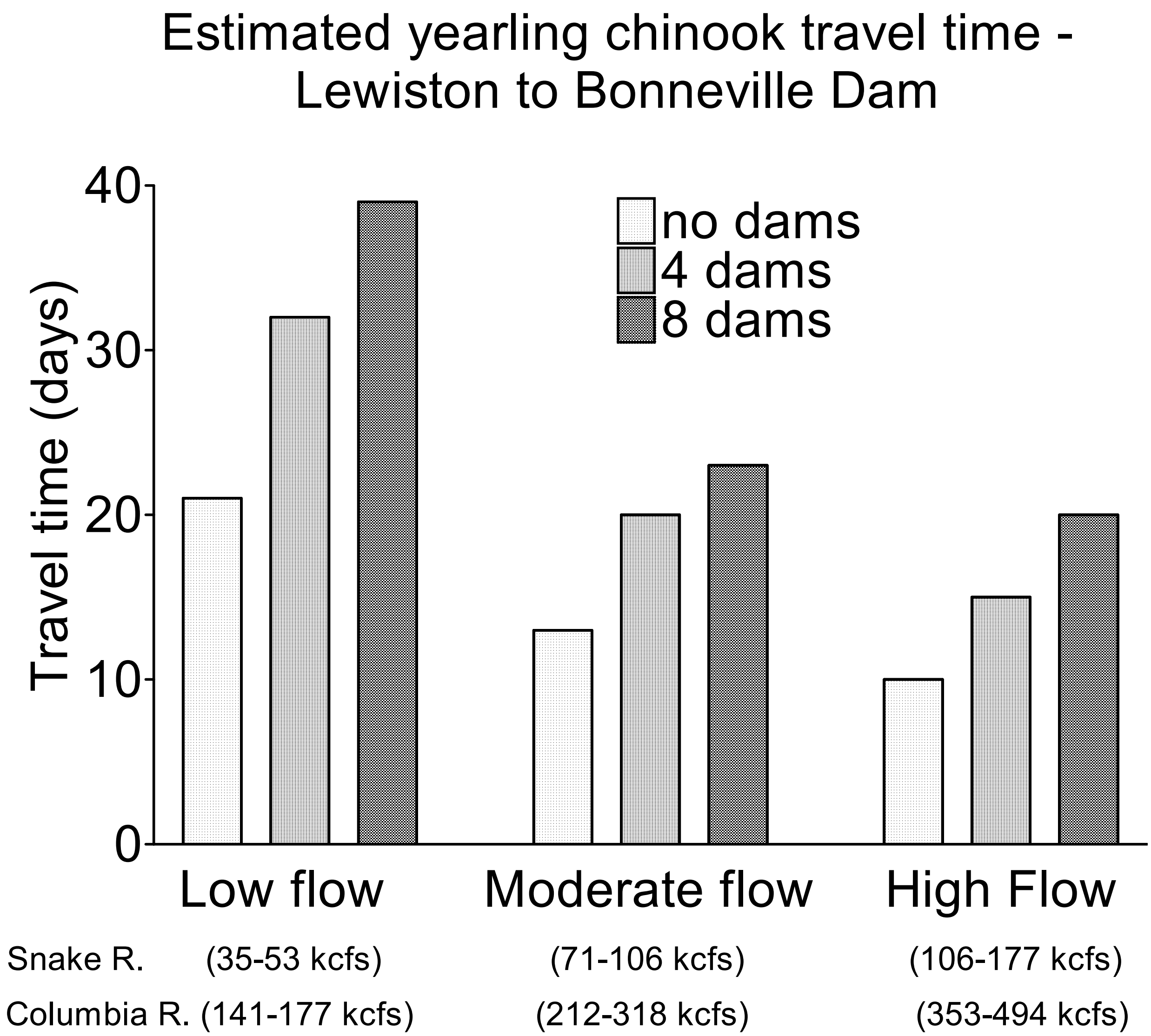


Figure 27. Estimated travel times for yearling chinook salmon through the section of the lower Snake and Columbia Rivers now inundated by mainstem hydropower dams (approximately from Lewiston, ID to the tailrace of Bonneville Dam). Estimates for the "no-" and 4-dam scenarios derived after data in Raymond {Raymond, 1979 #261}. Data for 8 dams derived from PIT-tagged fish between the period 1997 and 2003.

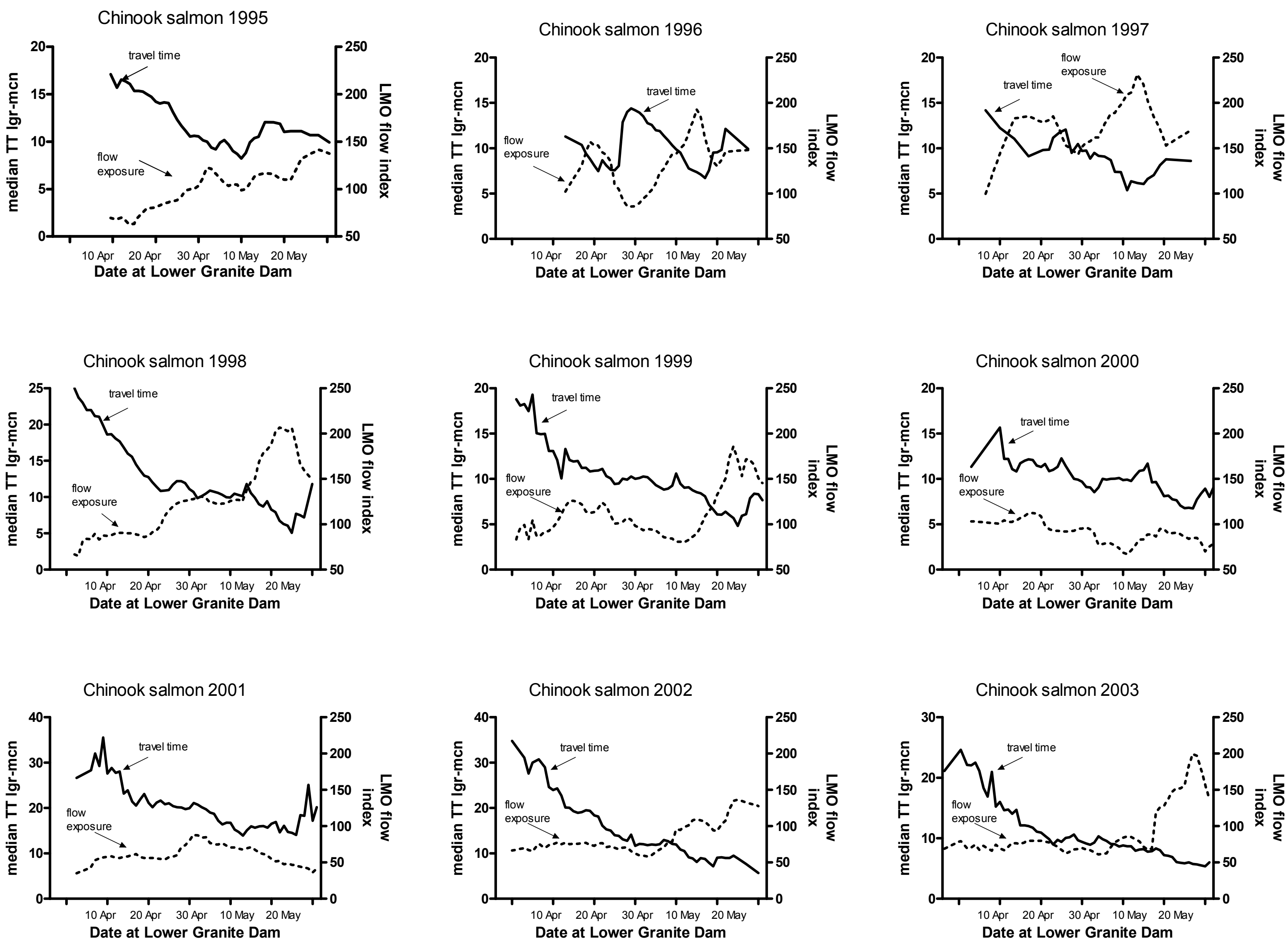


Figure 28. Median travel time and flow exposure index for groups of PIT-tagged Snake River yearling chinook salmon, 1995-2003.

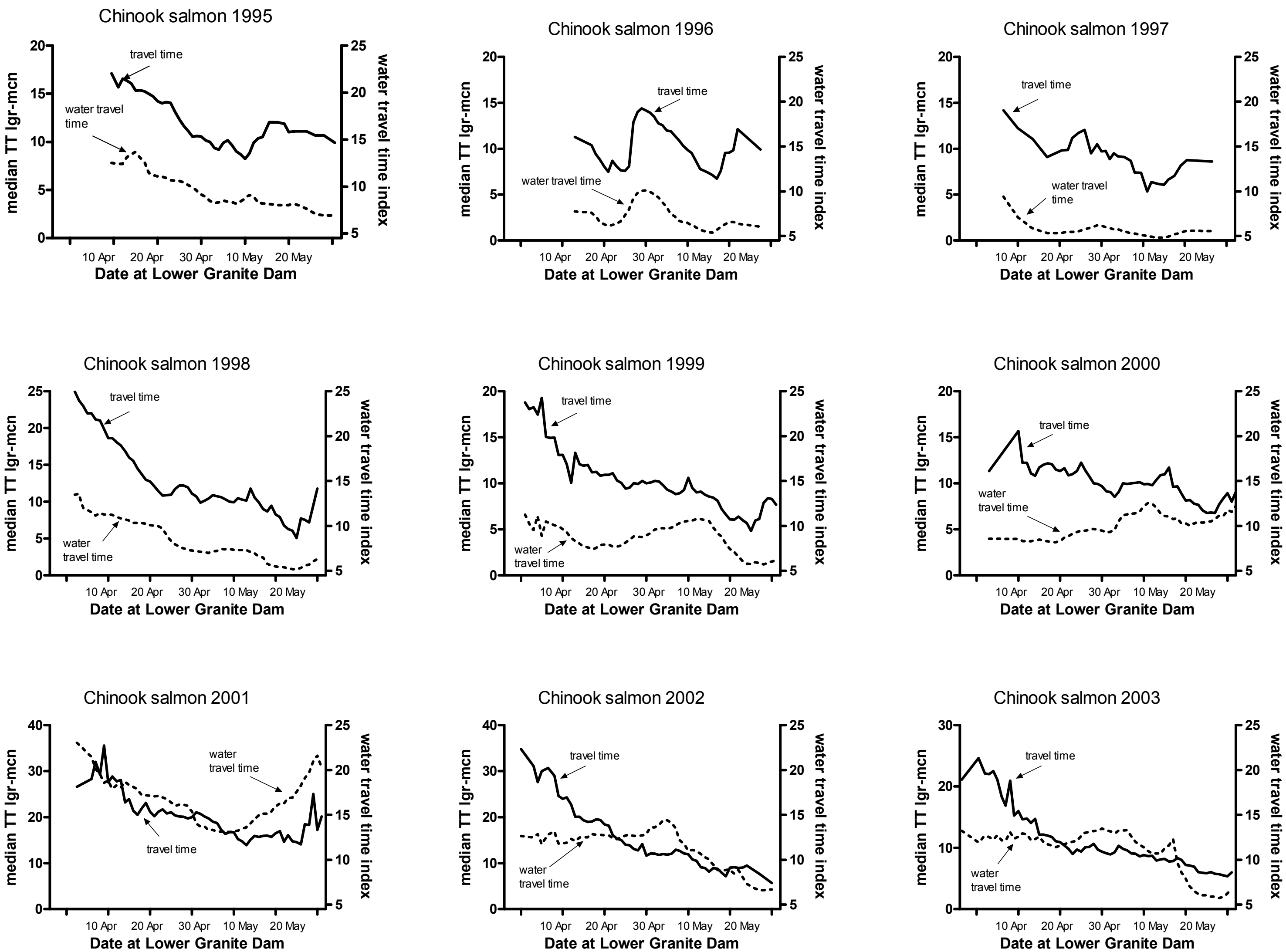


Figure 29. Median travel time and water travel time index for groups of PIT-tagged Snake River yearling chinook salmon, 1995-2003.

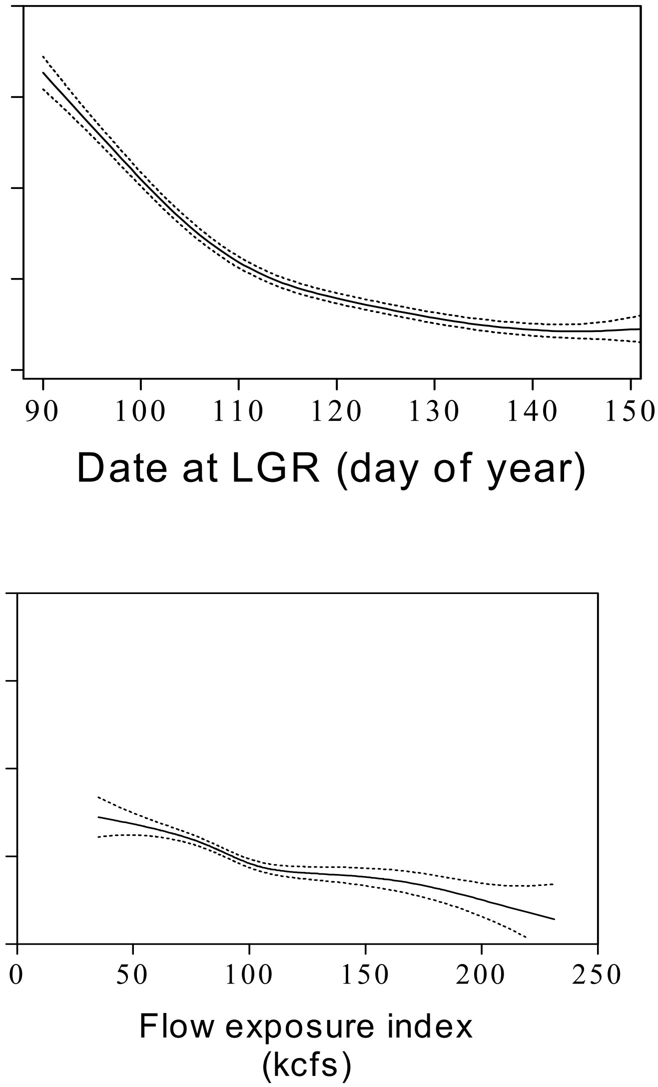


Figure 30. Partial fits for generalized additive model of median travel time from Lower Granite (LGR) Dam to McNary (MCN) Dam (days), with pointwise 95% confidence intervals, yearling chinook salmon, 1995-2003. Predictor variables were release date from Lower Granite Dam (LGR), flow exposure index (kcfs), and year effects.

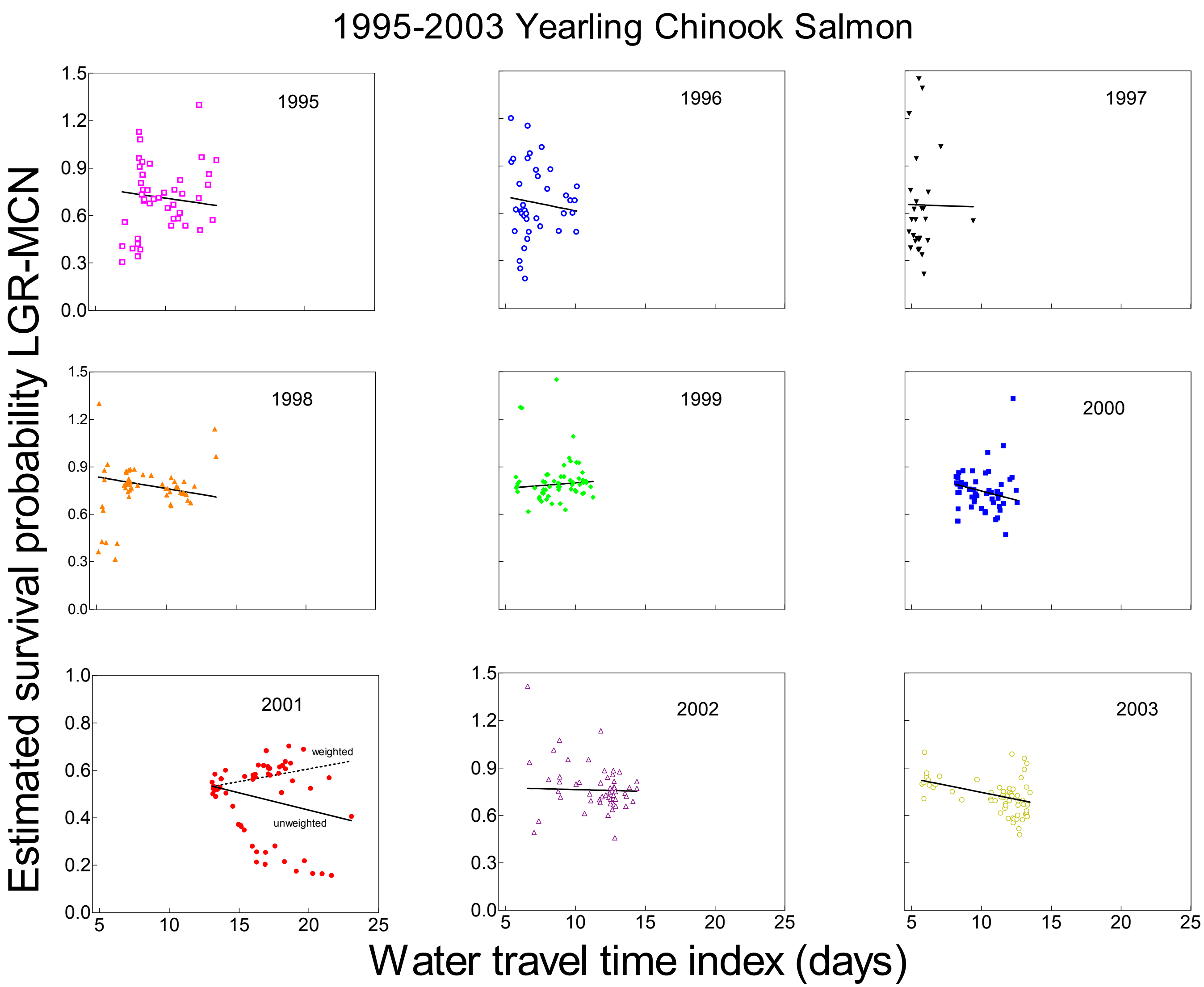


Figure 31. Estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake River yearling chinook salmon, plotted against water travel time index, 1995-2003.

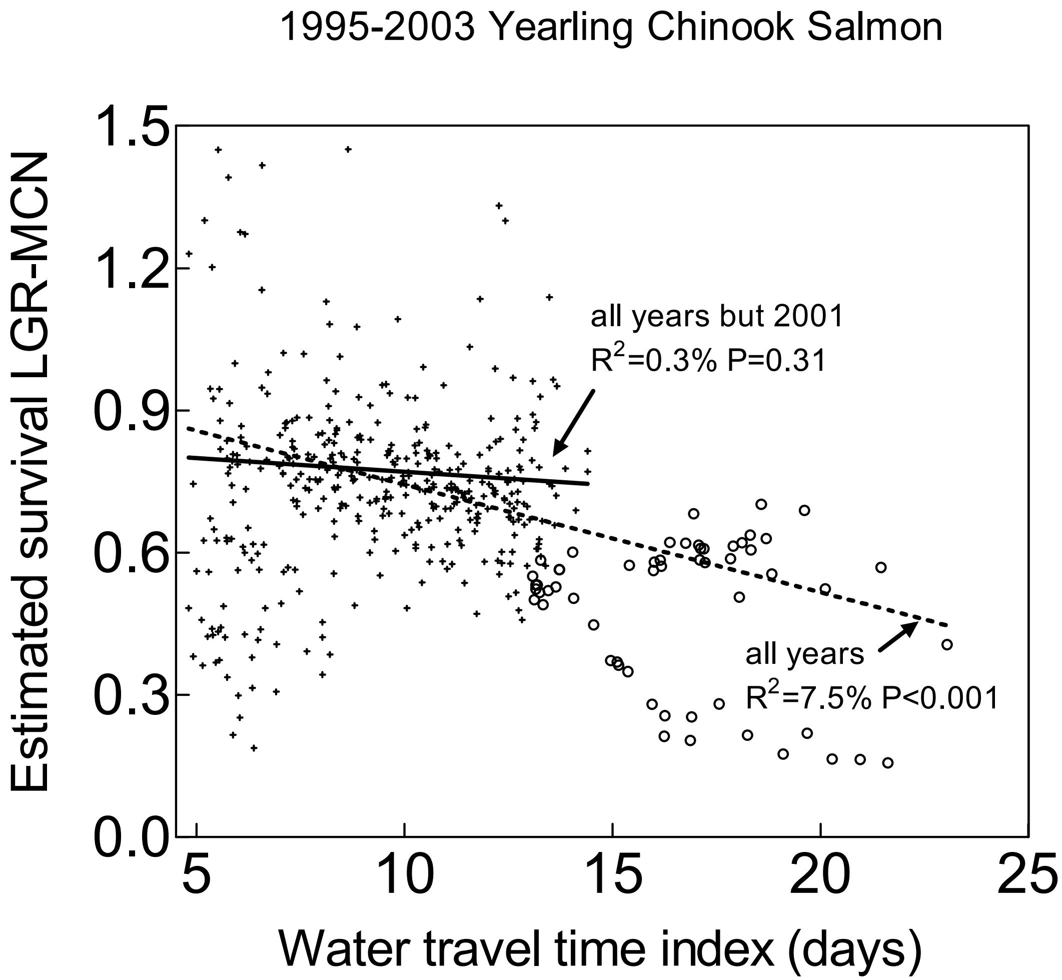


Figure 32. Estimated survival from Lower Granite Dam to McNary Dam vs. water travel time for PIT-tagged Snake River yearling chinook salmon, 1995-2003. Data from 2001 plotted with circles; crosses denote data from all other years.

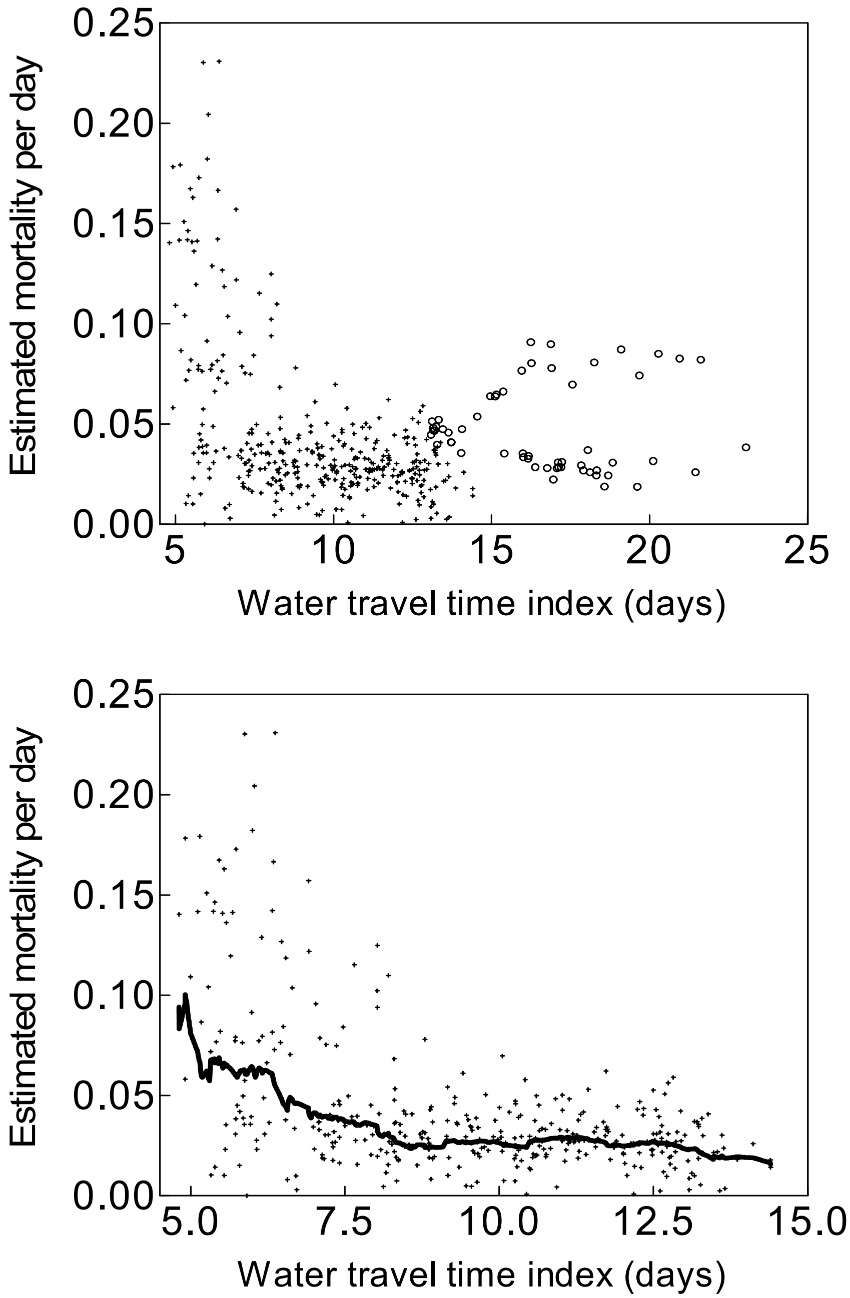


Figure 33. Estimated mortality per day vs. water travel time index for PIT-tagged Snake River yearling chinook salmon, 1995-2003. Top panel includes 2001 data (circles); bottom panel excludes 2001. Lowess smooth (black line) in bottom panel indicates that mortality per day tended to increase with decreased water travel time.

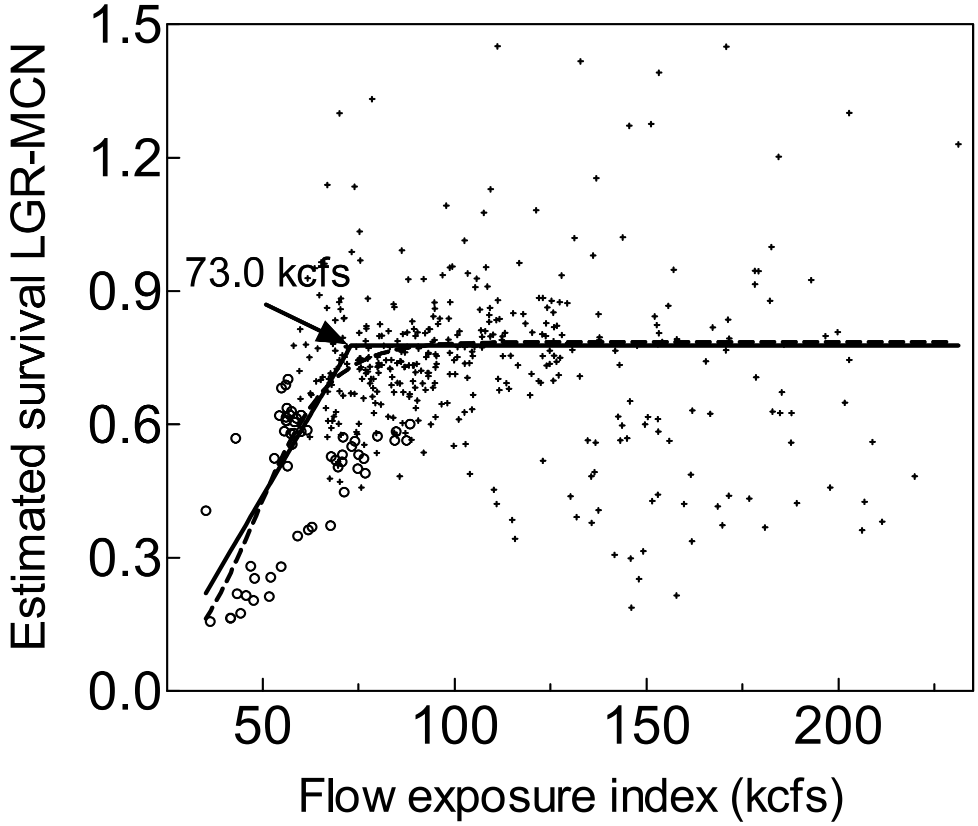


Figure 34. Best-fit sigmoid curve (dashed line) and broken-stick (solid line) for estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake River yearling chinook salmon vs. flow exposure index, 1995-2003. Data from 2001 are plotted with circles; crosses designate all other years. Point of "break" or threshold is estimated very imprecisely (see text).

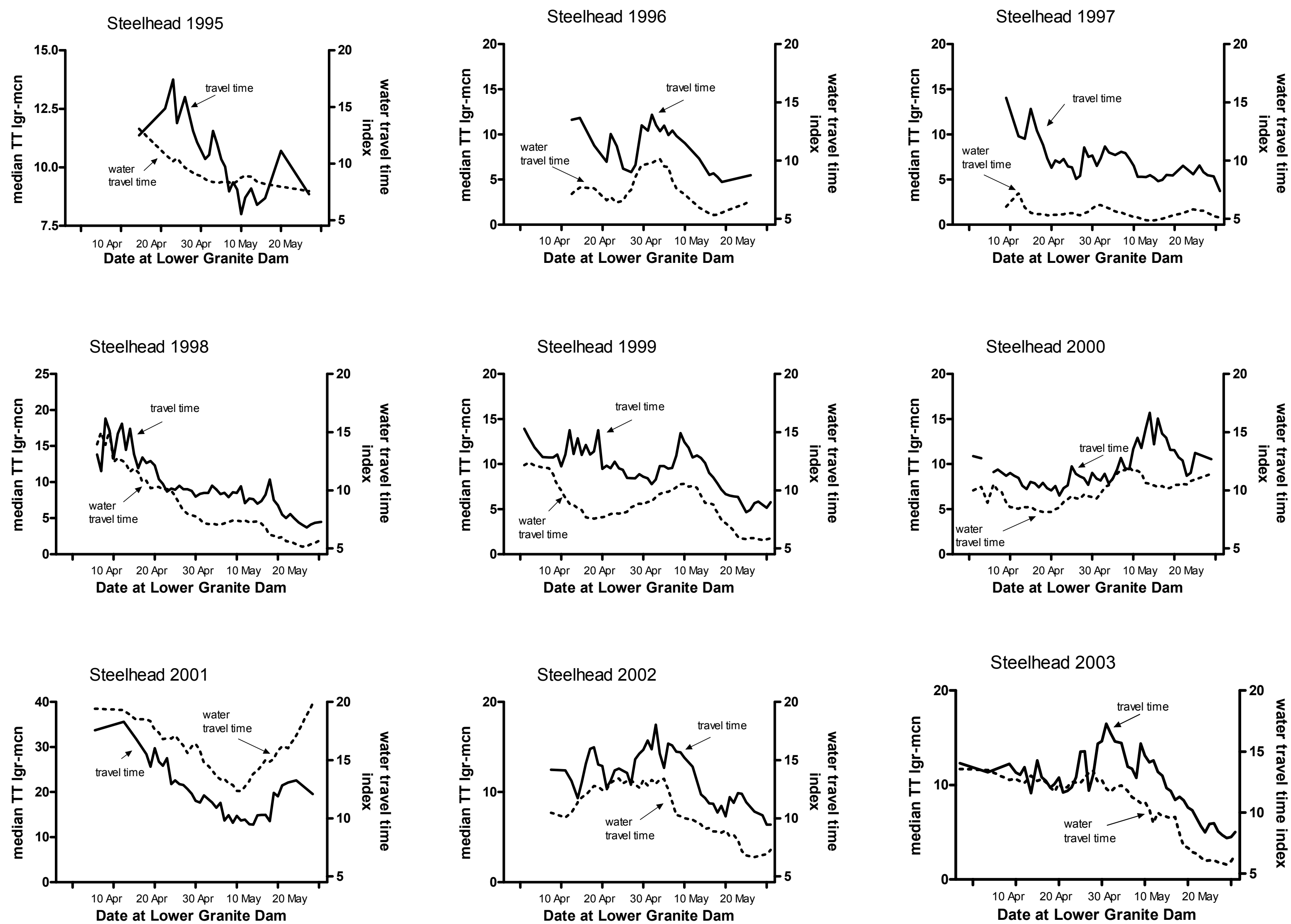


Figure 35. Median travel time water travel time index for groups of PIT-tagged Snake River steelhead, 1995-2003.

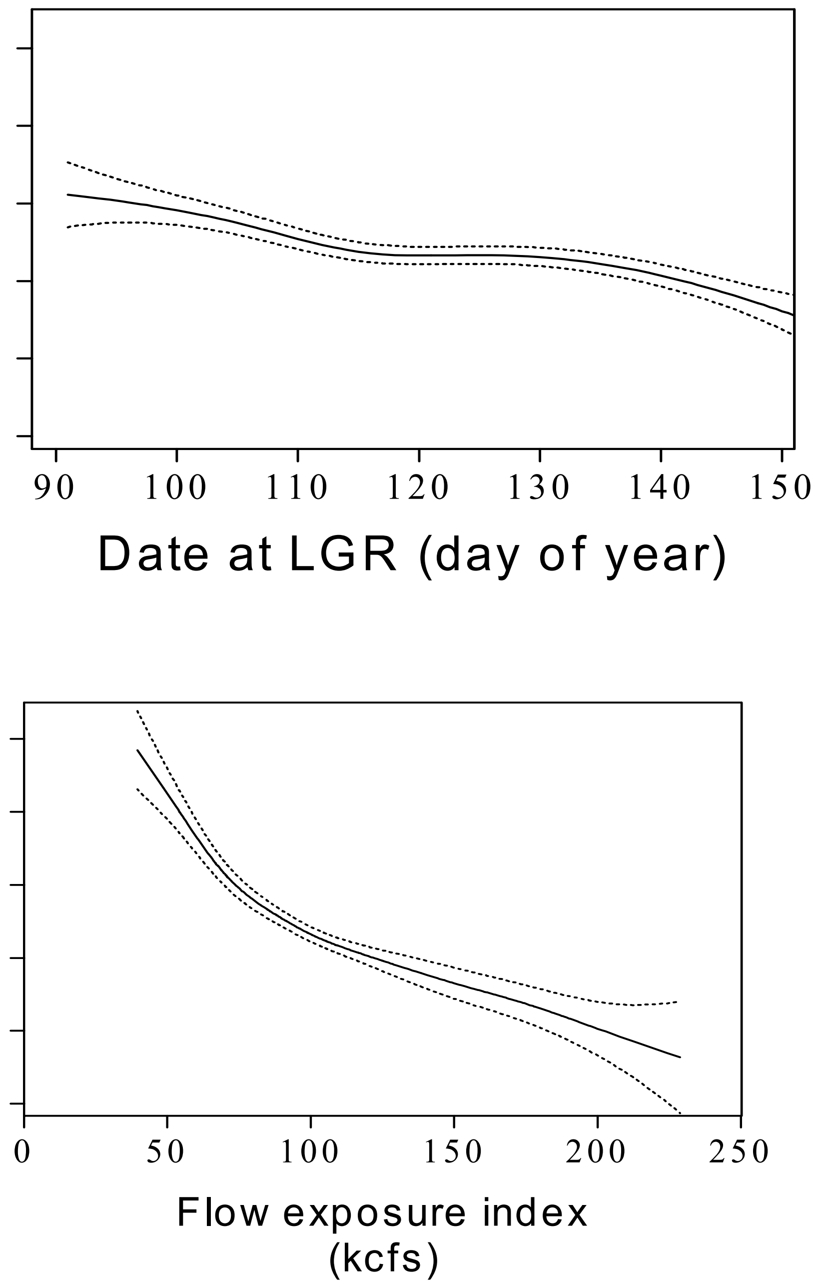


Figure 36. Partial fits for generalized additive model of median travel time from Lower Granite (LGR) Dam to McNary (MCN) Dam (days), with pointwise 95% confidence intervals, steelhead, 1995-2003. Predictor variables were release date from Lower Granite Dam (LGR), flow exposure index (kcfs), and year effects.

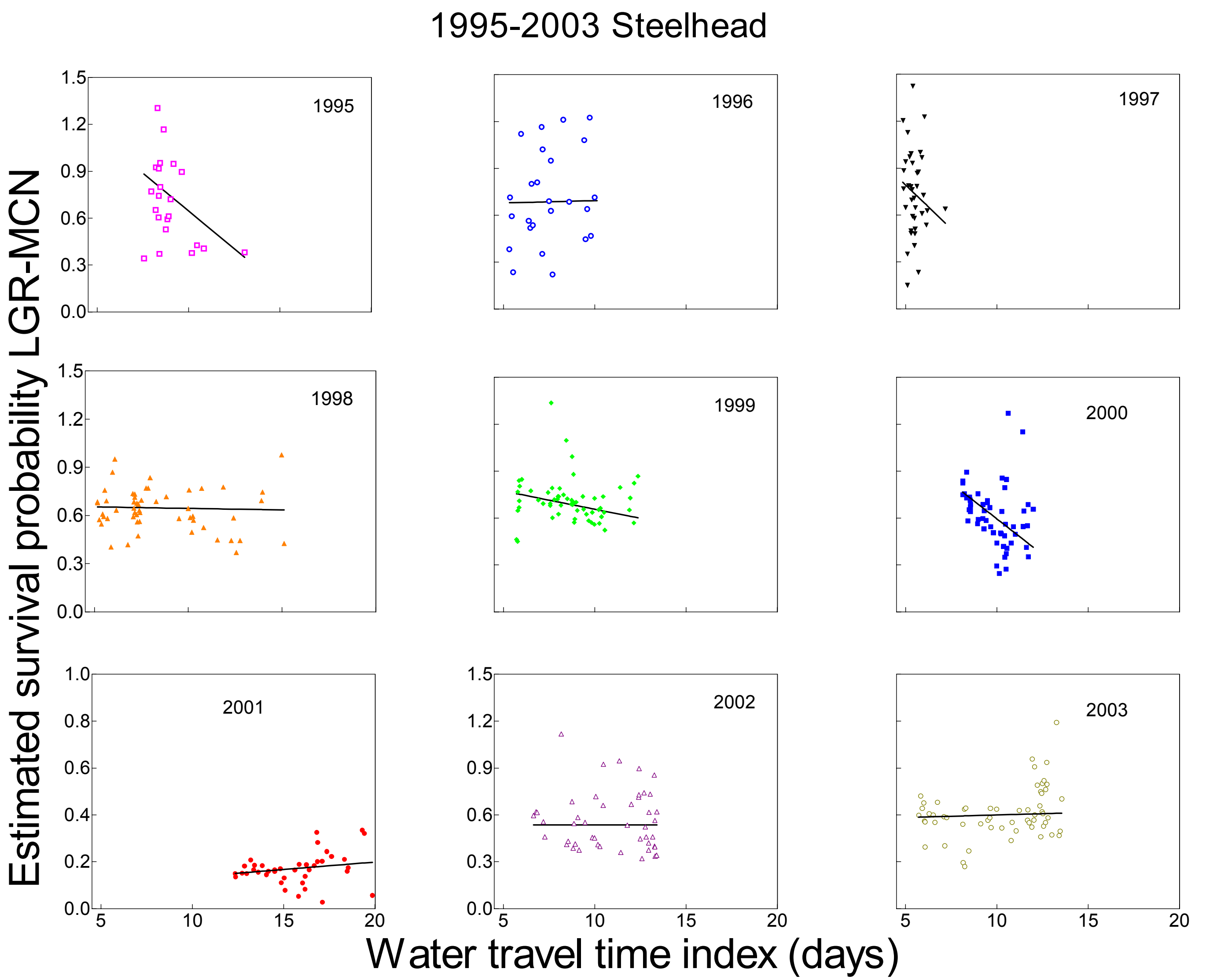


Figure 37. Estimated survival fmro Lower Granite Dam to McNary Dam for PIT-tagged snake River steelhead, plotted against water travel time index, 1995-2003.

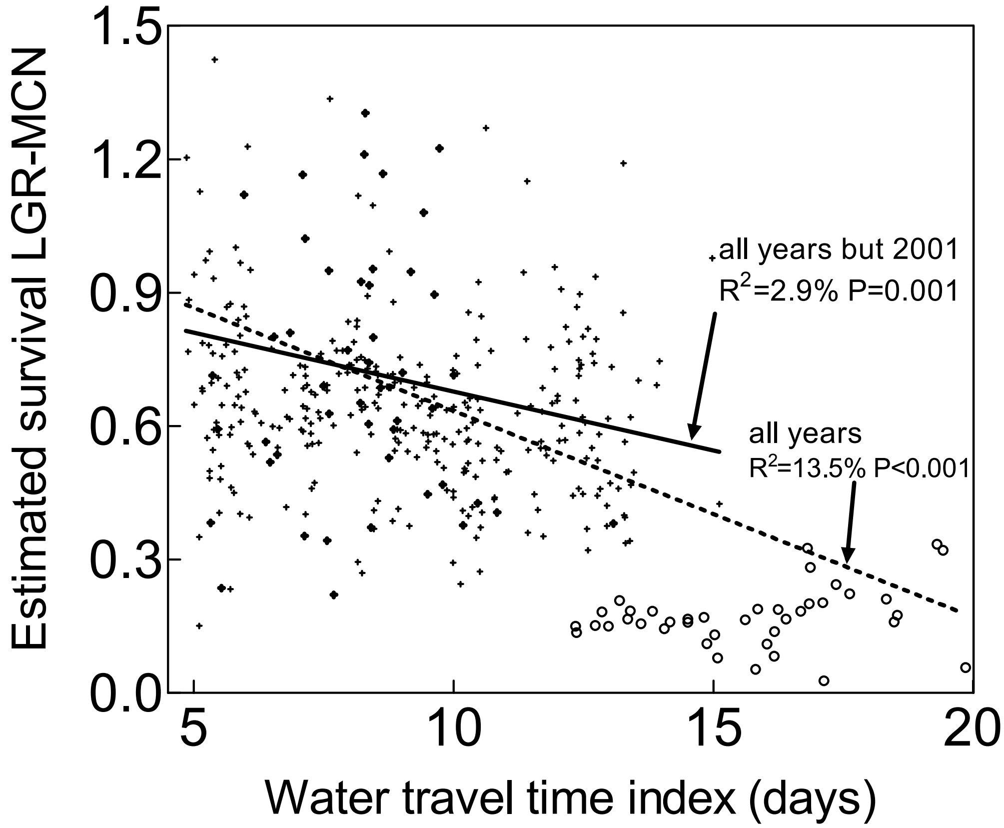


Figure 38. Estimated survival from Lower Granite Dam to McNary Dam vs. water travel time for PIT-tagged Snake River steelhead, 1995-2003. Data from 2001 plotted with circles; crosses denote data from all other years.

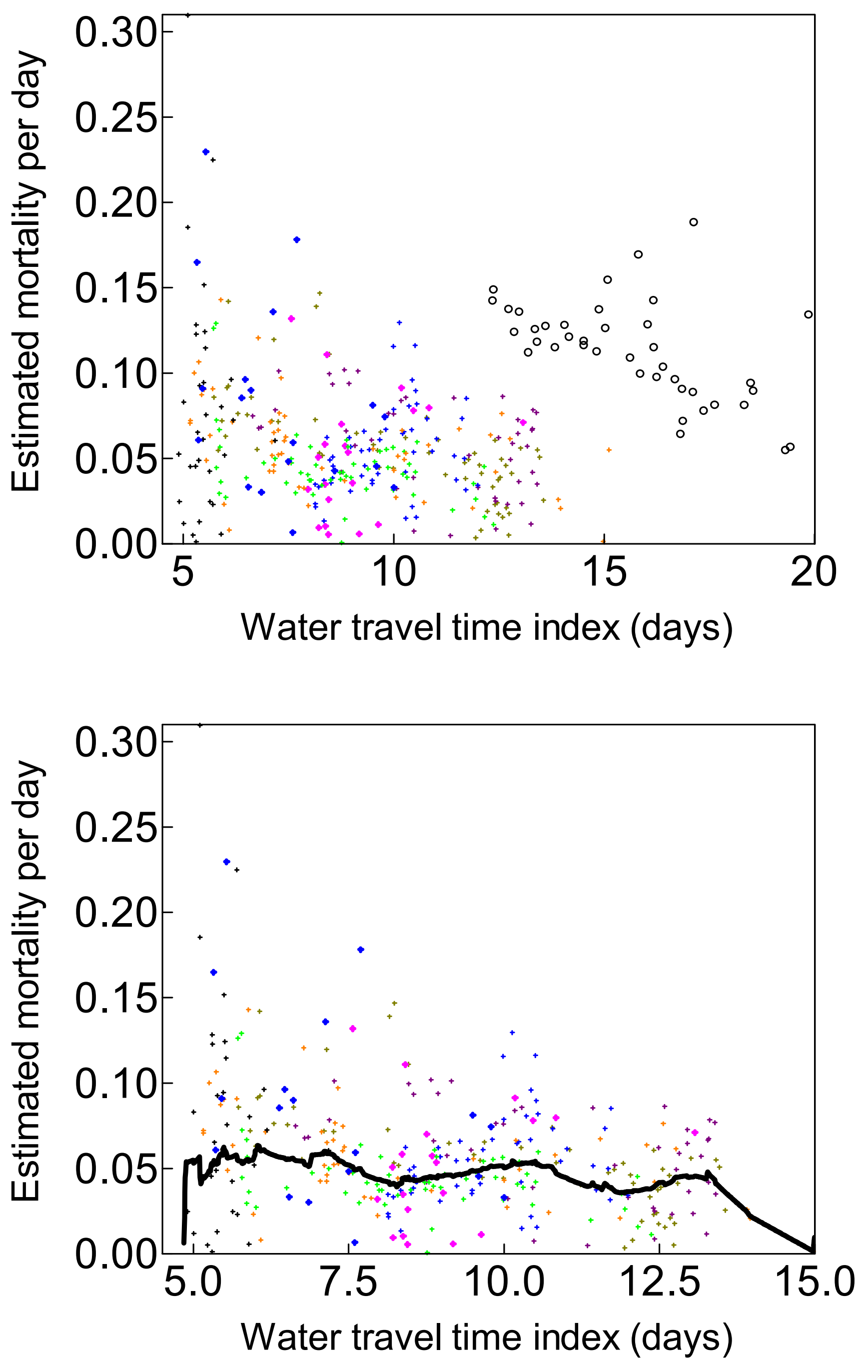


Figure 39. Estimated mortality per day vs. water travel time for PIT-tagged Snake River steelhead, 1995-2003. Top panel includes 2001 data (circles); bottom panel excludes 2001. Lowess smooth (black line) in bottom panel indcates that mortality per day was fairly constant at different water travel times, consistent with existence of both fish travel time/water travel time and survival/water travel time relationship.

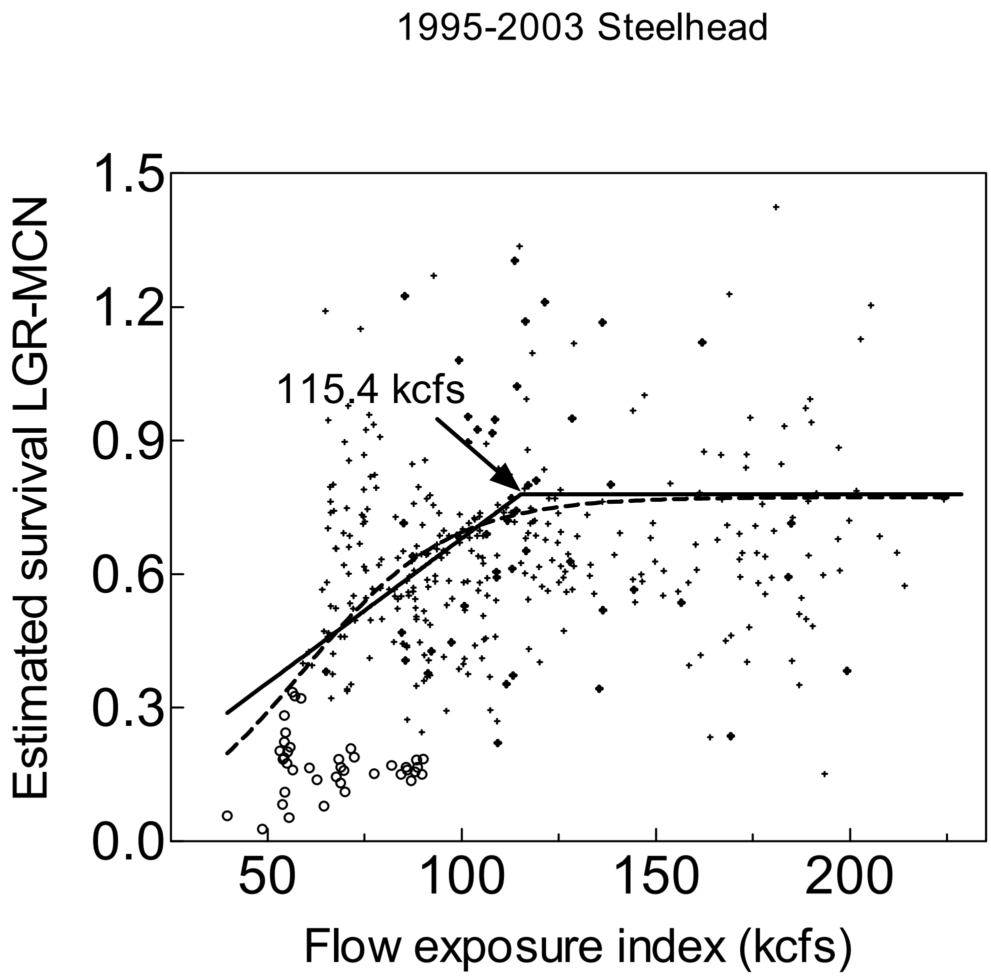


Figure 40. Best-fit sigmoid curve (dashed line) and broken-stick (solid line) for estaimted survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake river yearling chinook salmon vs. flow expposure index, 1995-2003. Data from 2001 are plotted with circles; crosses designate all other years. Point of "break" or threshold is estimated extremely imprecisely (see text).

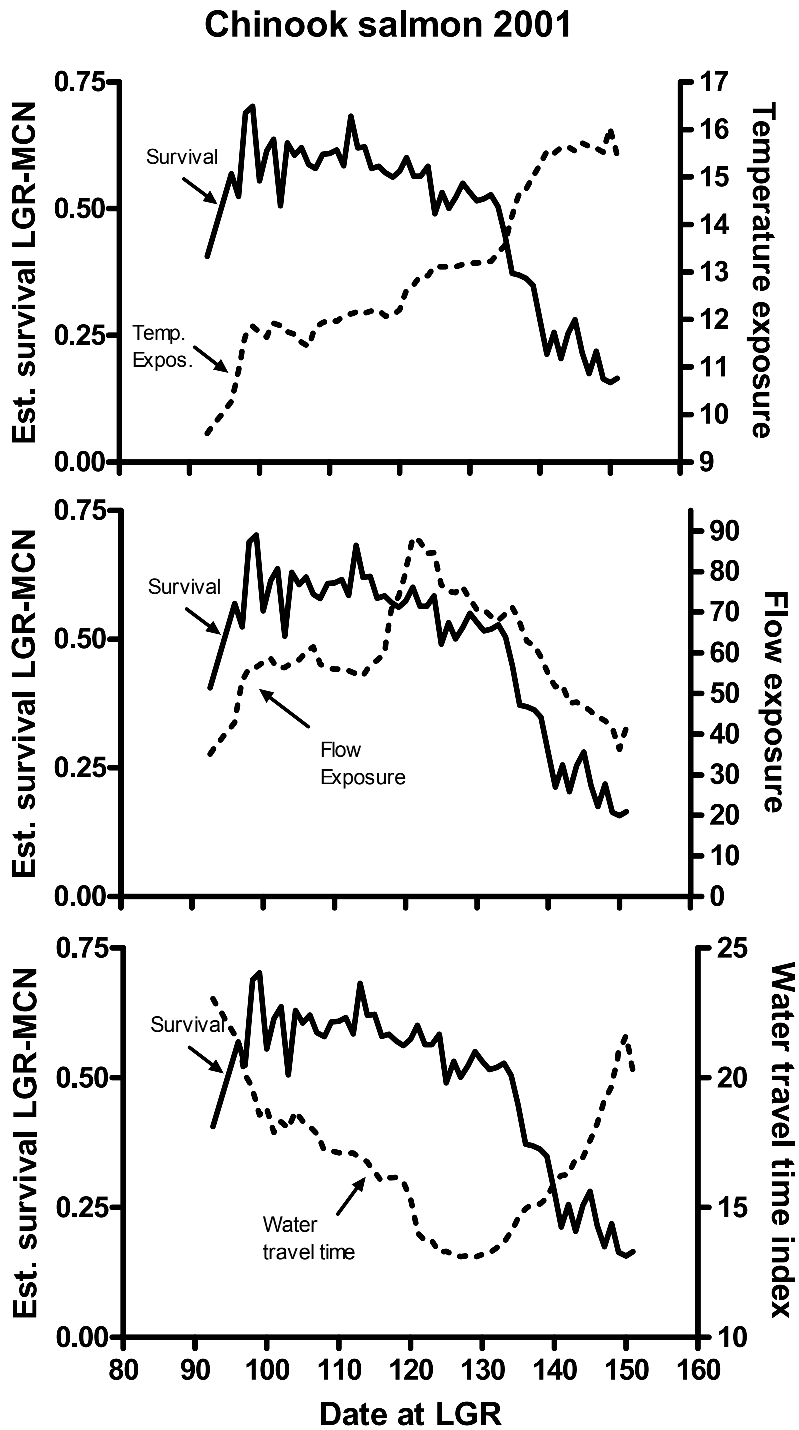


Figure 41. Estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake River yearling chinook salmon, 2001, plotted with flow exposure, water travel time index, and temperature exposure against date at Lower Granite Dam.

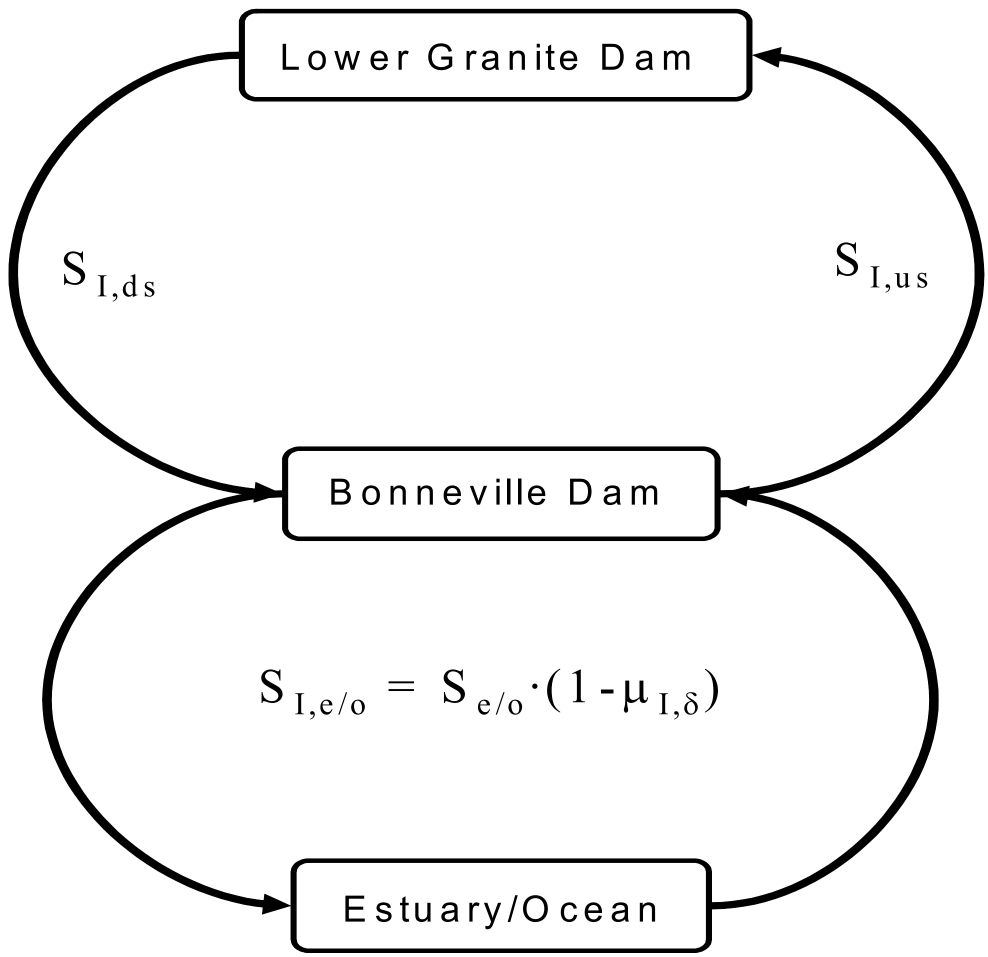


Figure 42. Survival (S) and mortality (μ) affecting Snake River anadromous salmonids migrating in-river (denoted by subscript I) at various life stages. The life stages are: downstream migration through the hydropower system (ds), estuary/ocean (e/o), and upstream migration through the hydropower system (us). The estuary/ocean survival is partitioned into survival that would occur in the absence of the hydropower system ($S_{e/o}$) and latent mortality associated with passage through the hydropower system ($\mu_{I,\delta}$). Transported fish (denoted by subscript T) are affected by the same survival and mortality processes and are represented by changing the subscript I to T.

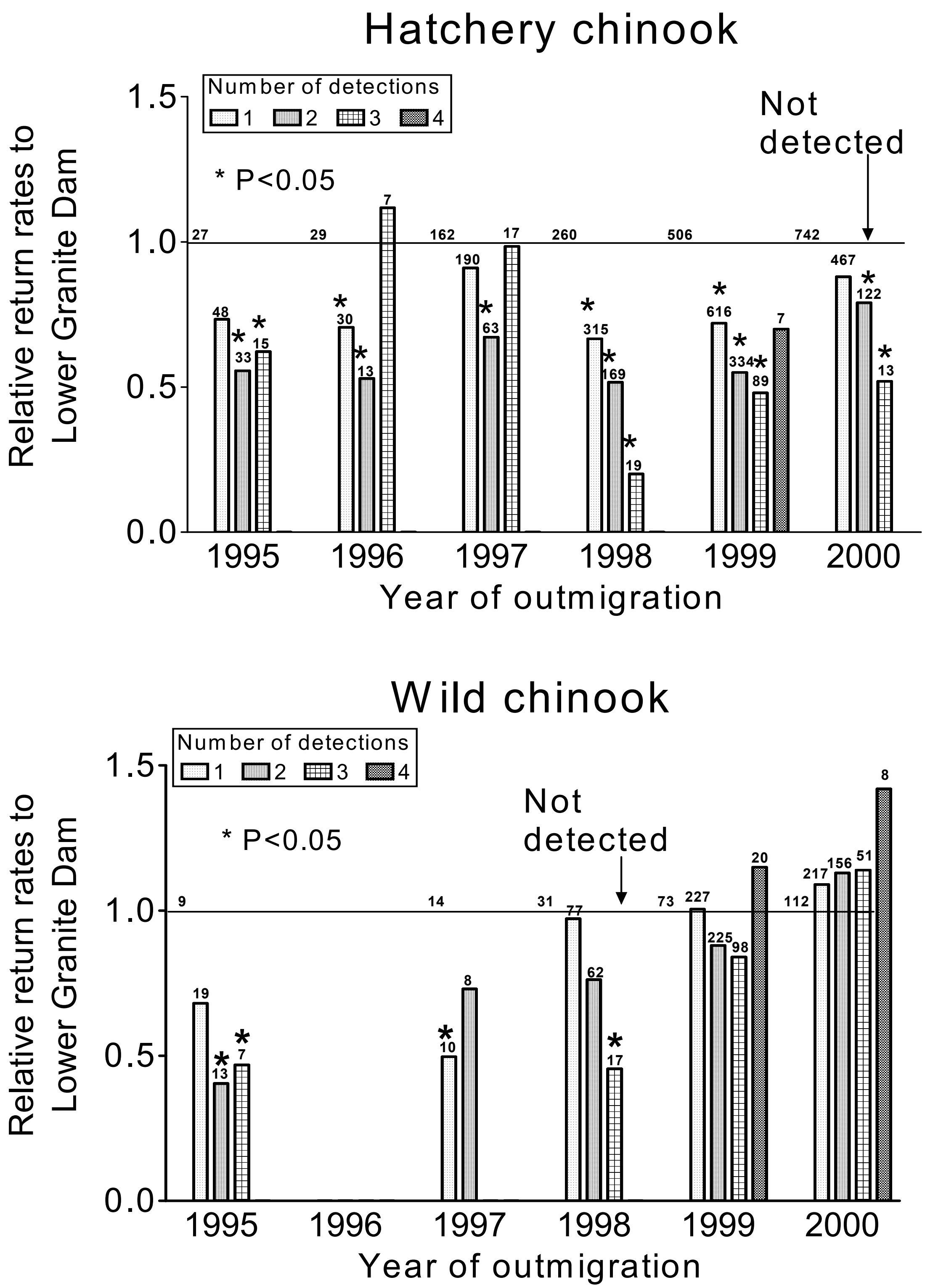
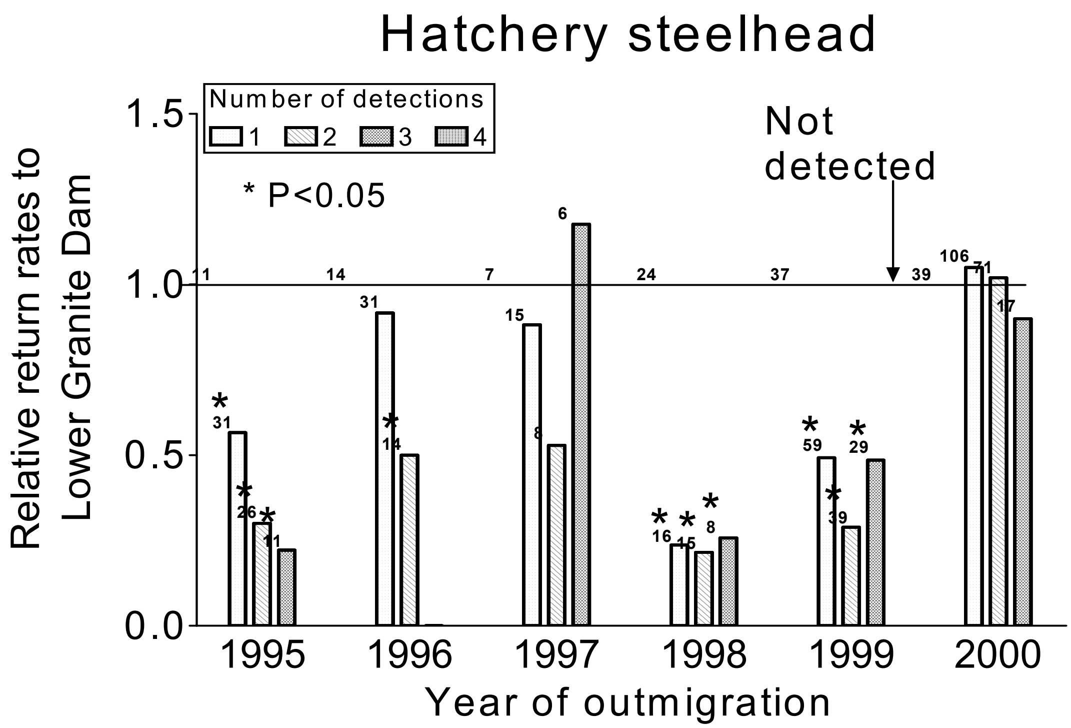


Figure 43. Relative adult return rates of hatchery and wild spring-summer chinook salmon marked above Lower Granite Dam and detected between 0 and 4 times during their migration through Lower Granite, Little Goose, Lower Monumental, and McNary Dams. Fish not detected as juveniles had a relative detection rate of 1.0.



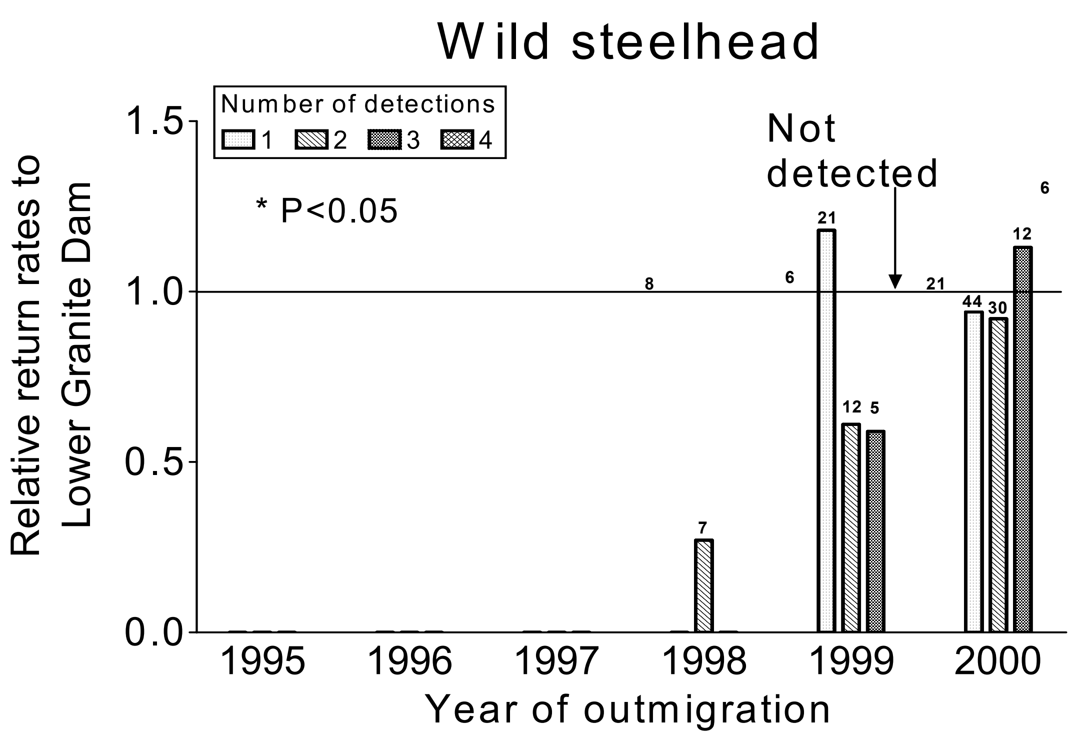


Figure 44. Relative adult return rates of hatchery and wild steelhead marked above Lower Granite Dam and detected 0 to 4 times during their migration through Lower Granite, Little Goose, Lower Monumental, or McNary Dams. Fish not detected as juveniles had a relative detection rate of 1.0.

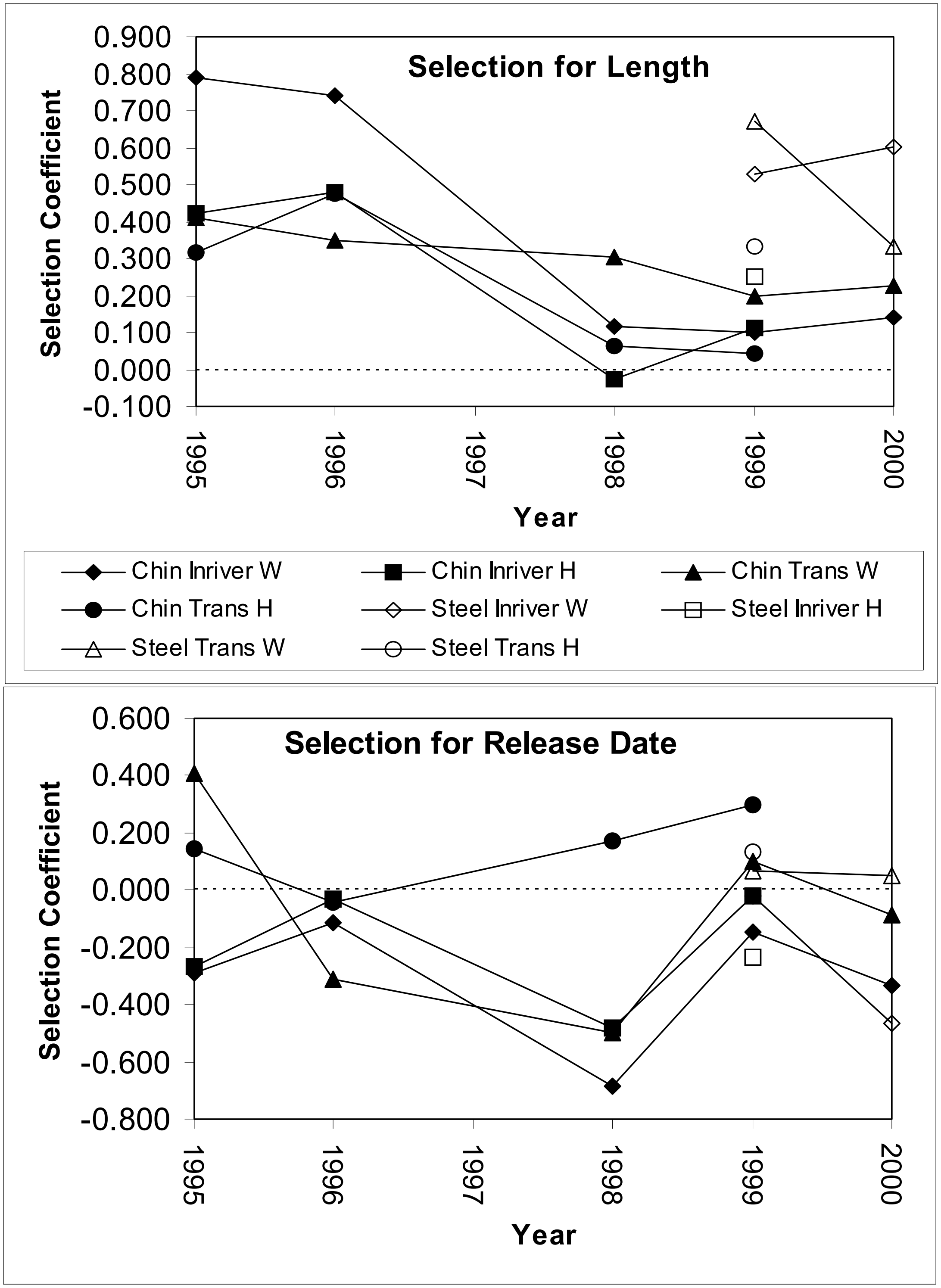


Figure 45. Selection coefficients (see text for details) by year for length at release (top plot) and release date (bottom plot). Abbreviations: Chin – chinook salmon; Steel – steelhead; Inriver – inriver migrants; Transport – transported fish.

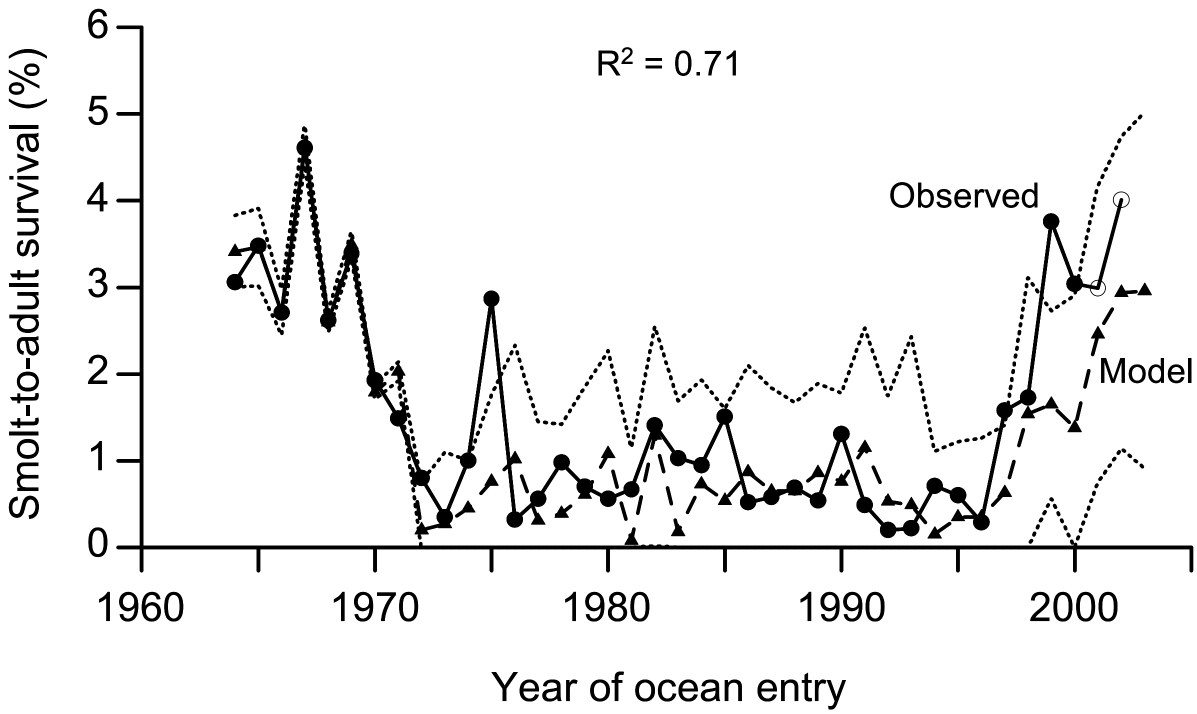


Figure 46. Time series of the observed smolt-to-adult survival (SAR) for wild Snake River spring-summer chinook salmon (circles) from 1964-2002 compared to the forecasts (triangles) from a time series model based on the coastal ocean upwelling index at 45˚N 125˚W. Dotted lines represent the 90% credible limits around the forecasts. Note that the SAR estimates for the 2001 and 2002 outmigrations (open circles) are preliminary in that they are based on age-3 (jack) returns in 2002 and age-3 plus age-4 returns in 2003. The forecast for the SAR for the 2003 outmigration is also shown.

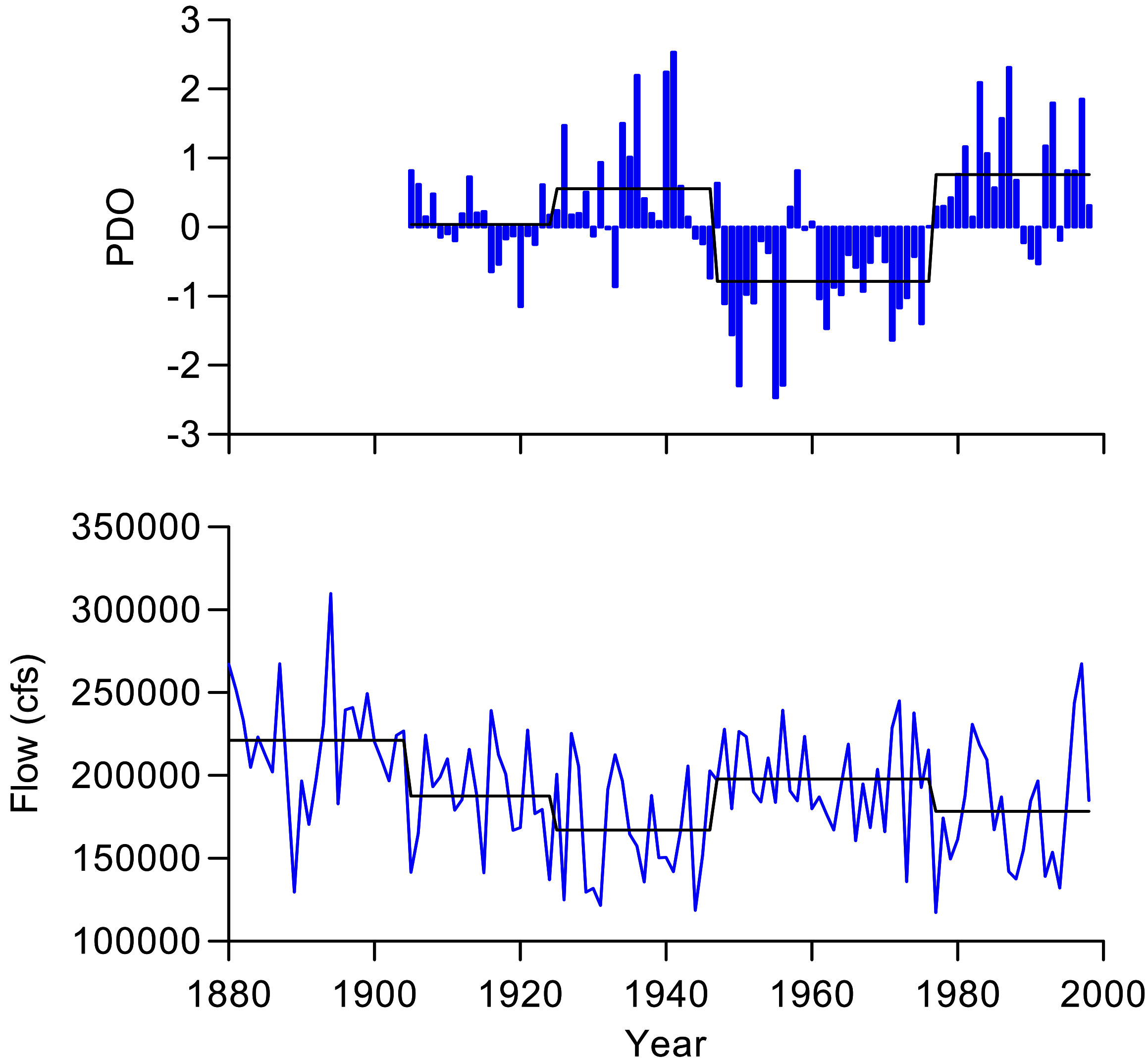


Figure 47. Normalized time series of the Pacific Decadal Oscillation (PDO, upper Panel) and Columbia River flow at The Dalles Dam (lower panel). The mean of each series over the various regime intervals as defined by Mantua et al. (1997) is superimposed to illustrate the ocean-land teleconnections evident in many climate processes. Note that when the PDO index is predominantly positive (e.g. 1977-1998), ocean conditions are deemed "poor" for Columbia River salmon. During these same time periods, river flows are also below the long-term mean.

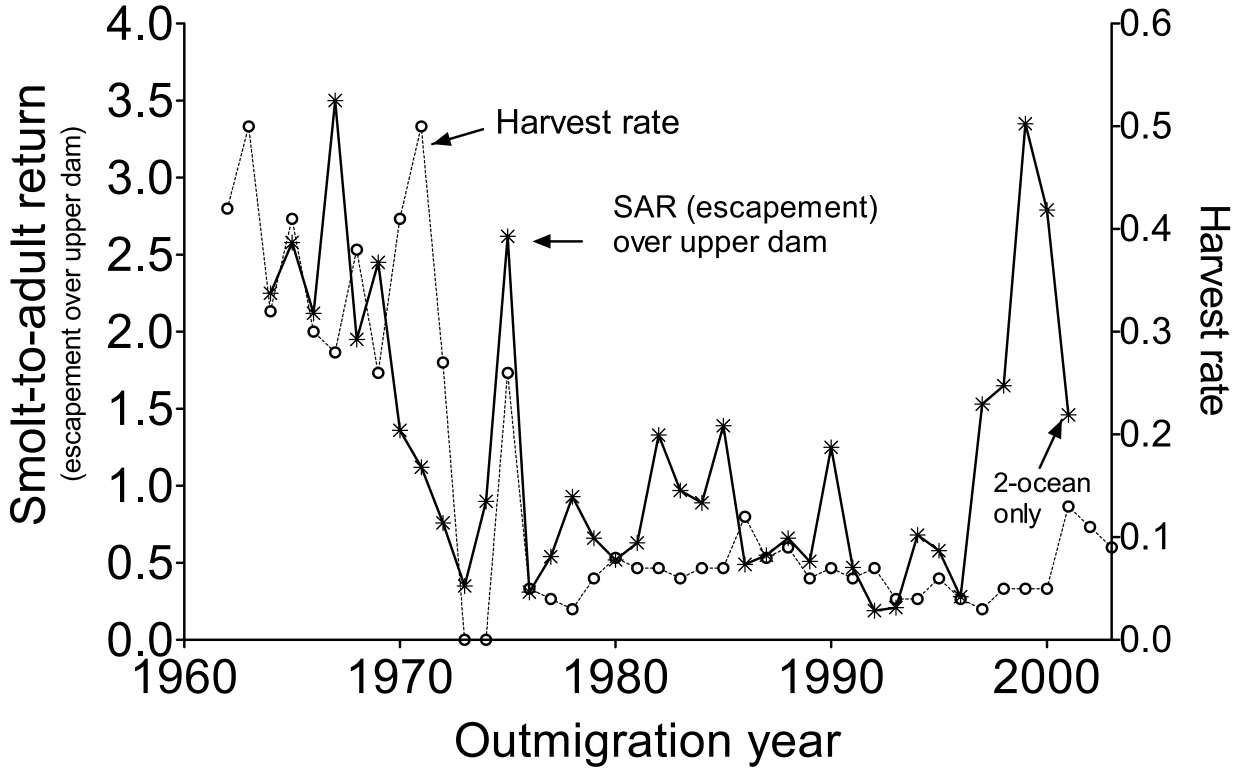


Figure 48. Estimated (escapement-based) smolt-to-adult return rate of spring-summer chinook salmon to the upper dam on the Snake River (solid line) and estimated annual harvest rate (dashed line).